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A SYNOPSIS OF THE AMPHIBIA OF CALIFORNIA

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CONTENTS

A SYNOPSIS OF THE AMPHIBIA OF CALIFORNIA

BY

TRACY I. STORER

(Contribution from the Museum of Vertebrate Zoology, and from the Zoological Laboratory of the College of Agriculture, University of California)

INTRODUCTION

The amphibians more than any other group of terrestrial vertebrates are dependent upon the presence of moisture for their successful existence, though different species vary greatly in the amount of water which is necessary for the completion of their respective life-cycles. The perennibranchiate urodeles and the American Bullfrog (*Rana catesbeiana*) can exist only in the presence of permanent bodies of water. In contrast to this some of the nocturnally foraging land salamanders (Plethodontidae) need nothing more than the humid atmosphere afforded by a cavity in a rotted log or the burrow of some terrestrial mammal; in such situations they can spend the daytime hours and, at the appropriate season, deposit their eggs. But the environmental requirements of the greater number of species of amphibians, at least in North America, are intermediate between these two extremes. They are truly *amphi* + *bios* (two-lived), requiring the presence of bodies of water for their egg, embryonic, and larval stages, but spending a certain portion of their lives out on the land. In some forms, such as the Spadefoot Toad (*Scaphiopus*), the aquatic stage requires but a few weeks; in others, such as the Marbled Salamander (*Dicamptodon ensatus*), a period of several months is passed in the water. Some species of Salientia are able to exist in the adult state in localities which afford a very meager amount of atmospheric or ground moisture. This is the case with the Spadefoot Toad (*Scaphiopus*) and some of the species of true toads which

inhabit the deserts of southeastern California and southwestern Arizona (as for example, *Bufo punctatus*). But all of these species require water for spawning purposes.

In eastern North America and western Europe, where the life-histories of amphibians, particularly the Salientia, have been studied in detail by numerous observers (see especially Wright, 1914, and Boulenger, 1897–98), the accumulated evidence goes to show that temperature is the most important factor in the environment. The time of emergence from hibernation in the spring and the time of egg deposition hinge closely upon the arrival of particular temperatures in the air or water or both. Below certain limits, which are different for each species, the animals do not leave their winter retreats. Once the appropriate minimum is reached their appearance may be expected with confidence. The findings of European and American investigators are in agreement on this point. Some species are evidently influenced by other factors in the environment, but these have not yet been investigated sufficiently if at all. One point is certain, however: the amphibians of eastern North America and western Europe are to be found in regions abundantly supplied with moisture through the season of their aboveground activity.

Study of the regulating conditions for amphibians in a semi-arid region, particularly one in which extremely low temperatures are rarely or never experienced but where the moisture relations are quite different, might be expected to reveal interesting adaptive responses on the part of the amphibians of the region. It was with this point in view that the present study was undertaken.

Studies on the life-histories of common amphibians, particularly the Salientia, involving the entire local fauna, have been carried on at Ithaca, New York, by A. H. Wright (1914), at Waco, Texas, by J. K. Strecker, Jr. (1908; 1910), and in California by the writer as detailed in the present paper. Wright's studies are by far the most complete of any which have been made in any one locality in North America, setting a standard toward which other workers in this field may well strive. Strecker's published data, save for three species, relate only to spawning seasons, and while very useful so far as they go, leave much still to be learned. They indicate in a general way the seasonal program of the amphibians in central Texas. The present writer's results are intended to outline the seasonal programs of the various species; the primary effort has been to learn the main points in the life-histories of as many species as possible. An endeavor has

been made to indicate the times and places where California amphibians may be sought so that investigators desiring to use these species for experimental purposes may hunt for them with expectation of success. It has also been hoped that, stimulated by the data here presented, other students may be attracted to the field and the life-histories of the California amphibians investigated in greater detail.

The climate of California, particularly of the interior valley and foothill districts, involves conditions widely different from those in eastern North America and western Europe. Here a rainy season of limited duration and characterized by moderate temperatures during the 'winter' months is followed by a long summer season of high daily (though moderate nightly) temperatures, with few or no summer rains and with low diurnal relative humidity.

This peculiar type of climate exercises a profound effect on the seasonal behavior of many different forms of life. Among mammals it has been found that the California Ground Squirrel *aestivates* during the latter part of the dry period, tiding over the season when food is scant in a resting or dormant condition analogous to that of arctic animals which *hibernate* when their food supply disappears or lies buried under snow. Many of the species of birds which nest in the territory where the semi-arid type of climate prevails react to the extreme dry season of the 'summer' months by migrating to more favorable locations. Among the so-called 'permanently resident' species of birds in the California foothills there are a number, such as the Spurred Towhee, Wren-tit, Bush-tit, and Vigors Wren, which each summer perform an altitudinal migration, moving in late summer up into the higher zones of the mountains where they continue until the rains break and induce a renewal of the food supply at the lower levels. Among the native insects some forms await the arrival of the rainy season for their breeding activities, thus assuring a sufficiency of moisture for the more susceptible egg and early larval stages. Of plants which are native to the 'semi-desert' conditions of interior California, many genera exhibit structural features, such as sclerophyllous stems and reduced leaf surface, which are of direct service in meeting a condition of limited water supply, while many species advance the seasonal program so that growth and blossoming is accomplished before the advent of the dry weather.

HISTORICAL NOTE

The first and in some ways one of the most important papers dealing with the amphibia of California was the fifth part of the Zoologischer Atlas issued in 1833 detailing the results of Dr. Friedrich Eschscholtz' visit to California in 1824. A few scattering specimens were obtained in the next two decades, but it was not until the advent of the Pacific Railroad surveys, following the discovery of gold in California, that the amphibian fauna of the State became known in any degree. The greater part of the material obtained by the naturalists attached to the survey parties came under the keen scrutiny of Spencer F. Baird and was described by him and his associates.

Subsequent literature dealing with the Amphibia of California is limited for the most part to portions of general articles dealing with amphibians in the western United States. The extent and nature of this material to date is indicated by the lists of synonymic references prefacing the accounts of species, taken in conjunction with the terminal bibliography. The several critical papers by Camp (1915–1917) dealing with local problems of classification and distribution which had vexed herpetologists for many years have done much to facilitate further studies in the local field. The check list by Grinnell and Camp (1917) was the first comprehensive paper on the amphibian fauna of the State. An excellent beginninig in the way of life-history studies was made with the appearance in 1897 of Ritter's paper on *Diemyctylus* [= *Triturus*] *torosus*, and this was followed by papers by Ritter and Miller (1899–1903) on the life-history of *Autodax* [= *Aneides*] *lugubris*. Here unfortunately the contributions end, save for a few scattering notes (Burke, 1911; Snyder, 1923; Van Denburgh, 1895*b*, 1898) on the eggs of other land salamanders. A few facts concerning life-histories of California amphibians are contained in Dickerson's Frog Book (1906).

MATERIAL

When the writer began to collect data on California species he found, therefore, an almost unexplored field. Numerous short field trips were made to seek out and identify the eggs and larvae of the aquatic spawning species occurring in the San Francisco Bay region;

then search was made in more distant localities for additional species. Trips were made to San Joaquin County in 1922, 1923, and 1924 for data on *Ambystoma californiense* and *Scaphiopus hammondii*, to Mendocino County in 1922 for *Dicamptodon ensatus*, and in 1923 a trip through the southern half of the State was made to study the various species occurring there.

With only a few species has it been possible to make the necessarily numerous visits to their spawning grounds to gather sufficient data for a satisfactory outline of the life-cycle. The conditions for study of these animals are very different in California from those obtaining in many places in the eastern states. Here, because of the arid nature of the country, the amphibians are usually quite local in occurrence and the investigator must hunt over large areas until thoroughly suitable locations are found. For example, at Berkeley, the nearest regular dependable spawning place for aquatic species was three miles distant, and only three species were to be found there. Other species required journeys of from 15 to 80 miles and it was seldom possible to plan field trips so that more than three species could be studied at one time. All of the specimens collected in connection with the studies of life-histories have been deposited in the Museum of Vertebrate Zoology. Where no authority is given for statements in the accompanying paper the author's personal field notes form the basis.

Acknowledgments

It is a pleasure to acknowledge the assistance which has been afforded the writer in his efforts to obtain data on the amphibians inhabiting California. The persons mentioned below have made special field trips at the request of the writer to look in 'likely' places for eggs or larvae of species which were especially desired. Miss Una Boyle of Calpella, Mendocino County, has aided in obtaining life-history material of *Dicamptodon ensatus;* Mr. Harry J. Snook of Stockton, *Ambystoma californiense;* Mr. L. N. Crawford of Santa Maria, and Mr. H. D. Badger of Betteravia, Santa Barbara County, *Scaphiopus hammondii;* Mr. Philip N. Baxter of Stockton, *Bufo b. halophilus;* Miss Sarah R. Atsatt of Los Angeles, *Hyla arenicolor;* Dr. P. E. Smith of Berkeley and Mr. Frank N. Bassett of Alameda, *Rana b. boylii;* Dr. Loye H. Miller and Mr. Alden Miller of Los

Angeles, *Rana a. draytonii;* and Mr. A. B. Haslacher of Farmington, San Joaquin County, *Rana catesbeiana.* Mr. and Mrs. J. E. Law helped in the prosecution of field work in southern California in the spring of 1923.

Dr. Charles L. Camp has kindly permitted the use of material from a manuscript on the amphibians of Los Angeles County which he prepared more than ten years ago. Authority for items quoted from this source is cited as "Camp, MS."

Dr. Loye H. Miller has placed at my disposal extensive manuscript notes which he made at Berkeley in 1898–99 and 1903–04 on the life-history and habits of *Aneides lugubris.* Material used is accredited as "Miller, MS."

The California Academy of Sciences has permitted the use of certain critical material from its extensive collections; general aid in many ways has been received from Dr. Joseph Grinnell and from other members of the staff of the Museum of Vertebrate Zoology; Dr. C. A. Kofoid of the Department of Zoology, University of California, has given valuable advice and criticism while the paper was in progress; and Ruth Risdon Storer has helped in the collection of material in the field, in the rearing of larvae, and in the recording of measurements.

GENERAL DISCUSSION

Amphibians are controlled in their distribution chiefly by conditions of temperature and moisture. The interplay of these two, in varying combination, sets the limits within which certain species may and others may not exist. Other factors are effective, at least in some cases, but a majority of species are limited by the two controls mentioned. Freezing temperatures can be withstood by amphibians for only brief periods of time; prolonged exposure results in death. The upper thermal death point for our amphibians is not known with any degree of accuracy. It varies greatly with different species. *Ascaphus truei* seems unable to withstand a temperature greater than 40° F. Some of our species seem to be able to withstand short exposure to temperatures up to 100° F. Ellis and Henderson (1915, pp. 254–255) report *Bufo boreas* in numbers in water at a temperature of 34° C. (93.2° F.). The limiting requirements with respect to moisture have already been indicated.

In the general geographic distribution of amphibians three factors have been postulated (see Gadow, 1901) as of prime importance in delimiting the ranges of these animals: salt water, permanently frozen ground, and complete deserts. The presence of large amounts of lime salts in the soil is also believed to be a barrier.

No marine species of amphibian is known. Salt water is in general an effective barrier to the entire group, though in diluted form it is at times inhabited by amphibians. Pearse (1911) has reported the successful development of ranid larvae in a branch of Manila Bay where the salinity was as great as 20.96 parts per thousand. The California Toad (*Bufo boreas halophilus*) has been observed on at least two occasions in the strongly brackish water at the head of San Pablo Bay; one individual was seen alive and swimming a quarter-mile from shore. Salt water, in combination with other factors, is at present operating to limit the range of certain species of amphibians in California. *Dicamptodon ensatus* and *Aneides flavipunctatus* occur in the coastal territory between the Golden Gate and Monterey Bay, but the individuals which live there are cut off from contact with the remainder of their respective species-

populations to the north by the salt water of San Francisco Bay. Due to the lack of suitable environmental conditions for these species by way of land around the eastern margin of the bay, San Francisco Bay and the Golden Gate may be said to constitute, at the present time, a barrier limiting their range. In the case of the island species, *Aneides l. farallonensis*, *Batrachoseps pacificus*, and *B. catalinae*, the salt water is an effective barrier, separating them from the mainland stocks to which they are most closely related.

No amphibian in California is limited by permanently frozen ground and, indeed, in North America generally there are at most only two species limited by that barrier. Five species of California amphibians occur in the Sierra Nevada up to altitudes of 10,000 feet or higher and thus have to meet 'boreal' conditions. These are *Hydromantes platycephala*, *Bufo boreas halophilus*, *Bufo canorus*, *Hyla regilla*, and *Rana boylii sierrae*. In the high altitudes reached or inhabited by these species there is a period of from several weeks to several months during the winter when low temperatures prevail. The frog (*Rana*), judging from its habits in summer, probably winters, like its overwintering larva, in the unfrozen water in the depths of the glacial lakes. The other species, which are primarily terrestrial in their habits, probably overwinter in holes in the ground or in crevices in rock slides. To judge from the amount of wintertime activity manifested by pocket gophers in the boreal portions of the Sierra Nevada (see Grinnell and Storer, 1924, pp. 139–140), there is but slight freezing of the ground. Hence, by retiring but a short distance below the surface these amphibians would be able to escape freezing. In the lower altitudes in California there is practically no danger to amphibians from freezing temperatures (see accounts of *Rana aurora draytonii* and *Rana boylii boylii*).

Complete deserts such as the Ṣahara of Africa and the Great Interior Desert of Australia are effective barriers to the spread of amphibians. The 'American deserts,' however, are inhabited in spots by several species of amphibians. Thus *Hyla regilla* occurs in several of the mountain ranges in eastern California; *Hyla arenicolor* lives in mountain cañons from Texas to California; *Bufo punctatus* is found in Death Valley and has been recorded from a cañon in the Turtle Mountains and in cañons on the west side of the Colorado Desert. Other species occur locally in the desert portions of Nevada,

Arizona, and New Mexico. The American deserts are believed to have evolved from an area that was much less arid in the recent past. A possible means of dispersal for the amphibians inhabiting desert areas, particularly cañons, is indicated in the account of *Hyla arenicolor.* The desert of southeastern California probably serves as a barrier to the spread of such a species as *Bufo alvarius* (the 'river' toad), which it would seem might be able to live in portions of the rivers of southwestern California, could it but reach that territory. *Scaphiopus couchii* now lives in southern Arizona and Lower California, but the desert of southeastern California (the Colorado Desert in particular) seems now to be too arid for the successful existence of this spadefoot there. Presumably it reached Lower California at a time when the Colorado Desert was less arid.

Certain Salientia in California regularly spawn and their larvae develop in ponds where the content of alkaline salts is exceedingly high. In Death Valley *Bufo punctatus* spawns in the alkaline waters from Texas Spring; in the Santa Rosa Mountains adults of this species were found in a creek the water of which was laden to saturation with alkali. On Carrizo Plain, in San Luis Obispo County, transforming individuals of *Scaphiopus hammondii* were collected in a pond the banks of which were encrusted with alkali deposited by the evaporating waters. These high concentrations of lime and magnesium salts do not seem to be effective in checking amphibians. In certain parts of the deserts of southeastern California where there are alkaline lakes amphibians are lacking, but I believe that the controlling factor in such cases is lack of suitable shelter for the adults and not the high concentration of salts.

Grinnell (1914, p. 252) has pointed out that, in the case of terrestrial birds and mammals, associational restriction of species is based upon three main items: (1) appropriate food supply, (2) presence of safe breeding places, and (3) presence of places of temporary refuge for individuals. As might be expected, the controlling conditions for amphibians, particularly the water-spawning species, are somewhat different.

Amphibians generally seem to exercise little choice in the matter of food. This is particularly true among the Salientia, as shown by the great range of items found in the stomachs of toads. The kind of food taken seems to depend largely, if not solely, upon availability.

A case is cited under *Bufo woodhousii* where an entire population of toads turned its attention to one particular source of food supply. Adults of *Rana a. draytonii* will regularly devour smaller individuals of their own kind *if* available; a successful 'frog farm' in California was maintained on the basis of this habit, it being easy to rear the young animals under artificial conditions. Yet in nature the same procedure on the part of the adults would lead rapidly to the extinction of the species. We cannot believe, therefore, that amphibians choose their food in the same sense that birds and mammals are known to do. Certain limitations in food are imposed by the sort of territory (ecologic niches) occupied by different species of amphibians; but differences arising in this manner are not to be considered matters of choice on the part of the animals themselves. The prime requirement of amphibians (except larval Salientia) in the matter of food seems to be that it shall be *moving*, that is, living.

The presence of safe, or better in the case of amphibians, suitable, breeding places is a factor of prime importance. As pointed out again and again in the accounts which follow, the adults of one species may occupy widely varying sorts of country, but they seek a particular kind of place in which to breed. A single pond may be the breeding place for three different species, provided, however, it is varied enough to offer the three special kinds of immediate surroundings which these species of amphibians require. Again, adult amphibians of certain species may live successfully, as individuals, in places where they do not have proper breeding facilities. Individual toads may live successfully in greenhouses or gardens in a closely built up city, but they cannot reproduce as a species unless suitable breeding places are available. Appropriate breeding facilities may not be available to a species every year; for example, certain ponds tenanted by *Ambystoma californiense* in 1922 and 1923 were completely dry in the winter of 1923–24. Yet if pools form, and persist for a sufficient period one or more times during the life-span of one group of mature individuals, the species will be able to persist. At Davis, Yolo County, in the spring of 1922, a particularly favorable pool produced an unusually large number of *Bufo b. halophilus*, for the bulk of the population seen in various daytime refuges in and about that town during the spring of 1924 consisted of two-year-old animals.

The matter of refuge for adults is highly important at all times to all amphibians. Some species, as for example, most of the true frogs (*Rana*), must be in the presence of water at all times. A certain few species such as the wood frogs (*Rana sylvatica* and *Rana cantabrigensis*) of eastern and northern North America are able to live on the damp floor of forests, but other ranas require marshes, streams, or ponds for their successful continuance *as individuals*, without regard to their respective *species* requirements in spawning. *Rana catesbeiana* is an extreme example, being able to persist only in the presence of permanent bodies of water. *Rana a. draytonii* is similarly restricted, the only apparent exceptions being where it lives in water tunnels the atmosphere of which is at all times saturated with moisture. Species of small size, such as *Hyla regilla*, can hide away in small crevices and so find in many places adequate shelter against desiccation, freezing, or capture by enemies; this particular species is therefore found in a great variety of surroundings.

The true toads (*Bufo*) and spadefoots (*Scaphiopus*) are provided with digging equipment (varying in development in the several species of the former group and developed to an extreme degree in the latter) whereby they are able to dig themselves suitable individual shelters in which to spend the daytime when the amount of atmospheric moisture is dangerously low. The species of terrestrial toads of the American desert (*Bufo cognatus* and *B. woodhousii* [pl. 11]) are provided with foot tubercles which, in appearance and hardness, resemble the 'spades' of *Scaphiopus* and are presumably used for the same purpose—to 'dig in' and avoid desiccation.

The salamanders, lacking suitable digging equipment, are found to inhabit places generally moist, and where natural crevices or other kinds of daytime retreats are available for the protection of the adults.

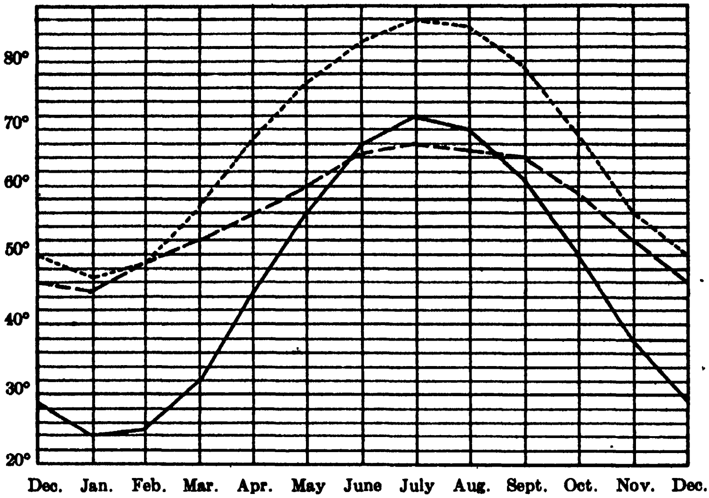


Fig. A. Mean monthly air temperatures (in degrees Fahrenheit) at Napa, California (— —); at Waco, Texas (- - - - - -); and at Ithaca, New York (——). Data from Henry, 1906, pp. 988, 429, 195.

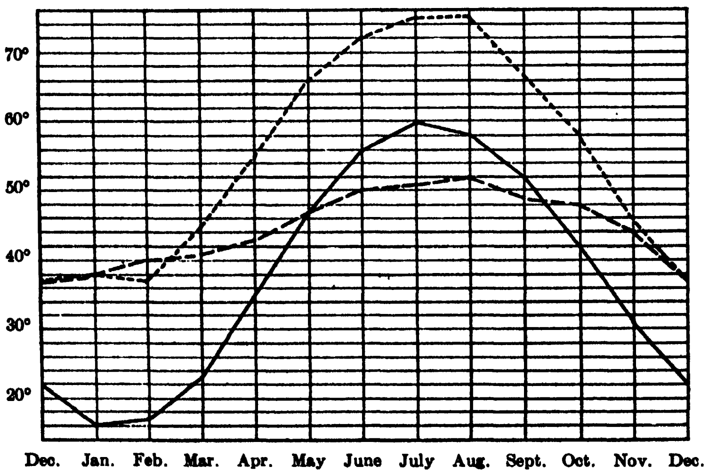


Fig. B. Mean minimum air temperatures (in degrees Fahrenheit), by months, at Napa, Waco, and Ithaca. See figure A for legend.

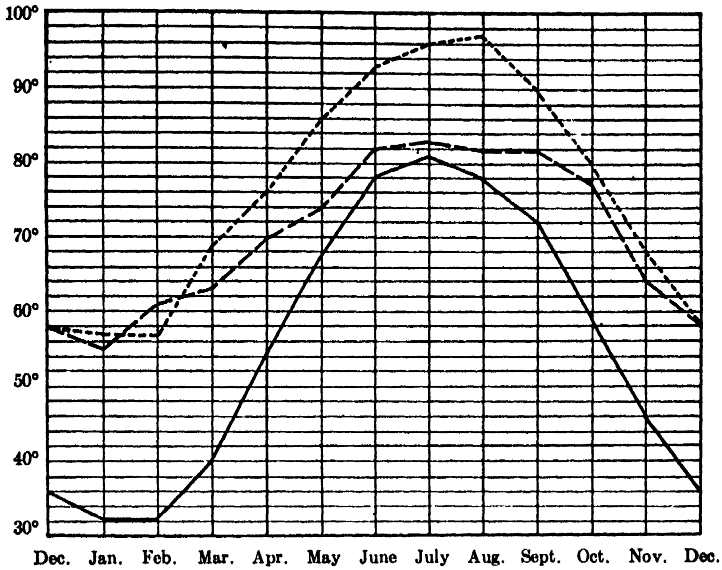


Fig. C. Mean maximum air temperatures (in degrees Fahrenheit), by months, at Napa, Waco, and Ithaca. See figure A for legend.

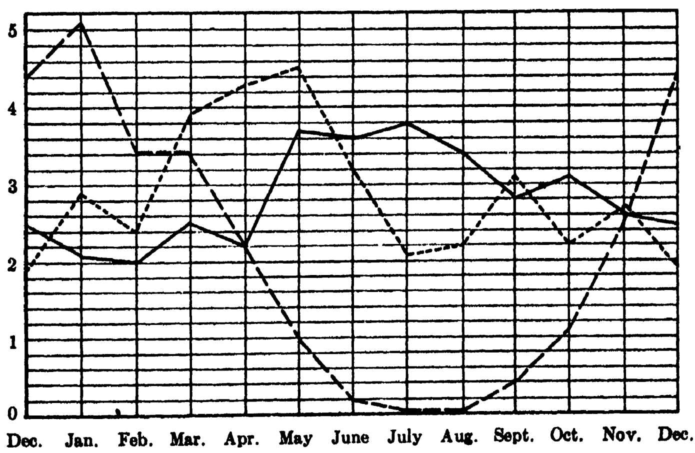


Fig. D. Mean monthly precipitation (in inches) at Napa, Waco, and Ithaca; See figure A for legend. Average annual precipitation (in inches): Napa, 23.7; Waco, 35.4; Ithaca, 34.4.

The climatic charts presented herewith (figs. A–E) indicate the seasonal fluctuations in temperature and moisture which are of importance to aquatic spawning amphibians, and, in some degree, to the land-spawning forms (Plethodontidae) as well. These charts are to be studied in connection with the chart showing the spawning seasons (fig. F). Data (from Henry, 1906) are presented for three stations, Ithaca, New York, representative of the northeastern United States, where Wright's (1914) observations were made; Waco, Texas, where Strecker's data (1908, 1910) were obtained; and Napa, California. The latter station, rather than Berkeley, was selected for reference in the present paper because it is more typical of the *average* conditions obtaining in interior California.

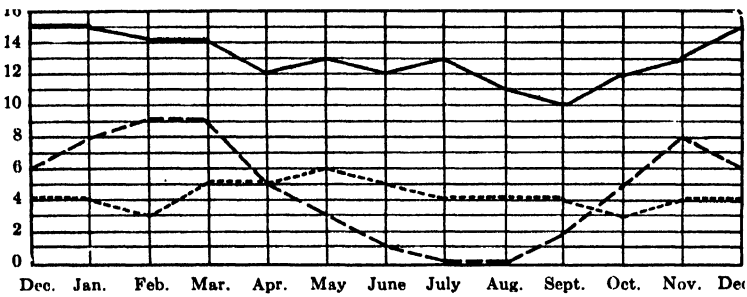


Fig. E. Number of days per month with 0.01 inch or more precipitation, at Napa, Waco, and Ithaca. See figure A for legend.

In brief, the climate at Ithaca (figs. A–E, ———), involves a winter cold season with low average, maximum, and minimum air temperatures (December to March), followed by a long period when even the air minima are high; the rainfall (including snowfall in terms of rainfall) is distributed through the year with an average of two inches or more throughout the summer season (April to September) and with an average occurrence of precipitation on 12 days per month during the growth period for amphibians. The summer season is therefore hot and moist.

At Waco (figs. A–E, - - - - - -), the temperatures of the winter period are high (above 40° F.), the summer maxima, minima, and averages are the highest of the three stations, the maximum rainfall comes in the spring (March to May), and the number of days per month on which rain falls averages close to 4 throughout the year. This is a hot climate, with optimum moisture conditions for the spawning of amphibians in the middle spring months.

The climate at Napa (figs. A–E, -- — —) is less varied with respect to temperature range than at either Ithaca or Waco, but the rainfall occurs during a much more limited period. None of the winter temperatures is low enough to restrict the spawning operations of amphibians. Conceivably, the animals could therefore breed at any season were moisture conditions suitable. But the rainfall is concentrated in the period from October or November until April; from May until September rain falls, on the average, on not more than three days per month and in total amount of one inch or less. The annual cycle shows low temperature amplitude, the midsummer temperatures approaching those of Ithaca, but there is a dry season not found at either Ithaca or Waco.

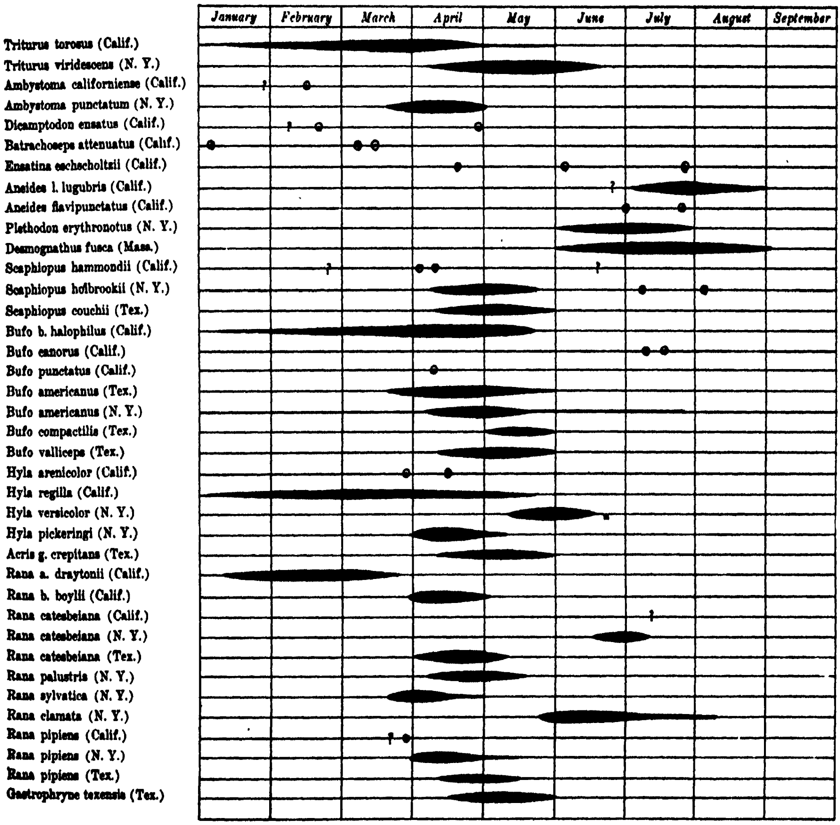


Fig. F. Spawning seasons of amphibians in California, central Texas, and western New York. Data for California from text of present paper; for Texas, at Waco from Strecker, 1908, 1910; for New York at Ithaca, from Wright, 1914. Individual items as follows: *Triturus viridescens*, Gage, 1891; *Ambystoma punctatum*, Wright and Allen 1909; *Desmognathus fusca*, I. W. Wilder, 1913; *Plethodon erythronotus*, Reed and Wright, 1909.

The spawning seasons of the California species (see fig. F), are advanced two to three months ahead of those of the species in Texas and New York. The only species which spawn in California during the summer months do so by reason of special adjustments in the matter of moisture.

The amphibians, because of their dependence upon conditions of temperature and moisture, are highly suitable material for indicating differences between various environments with respect to these factors.

Normally, the egg and larval stages of Salientia develop in water. Sampson (1900), however, has described the breeding habits of a number of exotic Salientia which in one way or another depart from the conventional method. Some species deposit their eggs in a mass of froth suspended above water; others, such as the Surinam Toad (*Pipa americana*) and the Obstetrical Toad (*Alytes obstetricans*) of southwestern Europe, carry the eggs or young for longer or shorter periods of time. In the tropical rain-forests, where much of the animal life is restricted to the arboreal habitat and where terrestrial pools of water are at a premium, certain species of Salientia pass both the *egg and larval* stages in the protecting coat of gelatinous material, 'hatching' as perfect though miniature replicas of the adult (see Noble, 1923). The atmosphere there is sufficiently humid so that there is no danger of desiccation to eggs laid out of water.

Hall (1922) has made an experimental test of the vital limit of exsiccation in various animals, including one species of frog (*Rana pipiens*) and a species of salamander (*Ambystoma punctatum*). By confining the animals in a chamber supplied with a current of well oxygenated but dried air, it was found that a frog could be reduced to a condition of apparent death (the skin becoming dry) with a loss of 50 per cent of the water contained in the body or 41 per cent of the total live weight, after which it would recover upon being placed in water. The salamander showed similar ability to withstand desiccation—loss of water up to 47 per cent of the body weight being followed by recovery upon immersion in water. In one instance an exsiccated animal when returned to water regained 97.7 per cent of its loss within 24 hours. It would be of great interest to determine the vital limits of exsiccation for some of the species of amphibians discussed in the present paper; *Rana pipiens* is a marsh-inhabiting frog and could scarcely be expected to exhibit so high a degree of resistance to loss of water as some of the desert toads.

The principal reactions to the dry climate of California are manifested in restriction of spawning to the rainy period, in abbreviation of the time spent in egg and larval stages, in the thickening of the skin in the adults, and in the development of digging spades whereby the animals are able to burrow into the ground for protection from desiccation during the dry period.

Cope has already remarked that the western species of *Rana* are thicker skinned than the frogs of eastern United States where the climate is more humid. It is of interest to note that within the *aurora* group of pond-inhabiting frogs here in the west, the northern form, *Rana aurora aurora,* which inhabits the northwestern humid coast district, has a relatively thin and smooth skin, whereas the southern and interior subspecies, *Rana aurora draytonii,* while also an inhabitant of ponds but in regions where the summer air is drier, has a roughened and thickened skin, the texture approaching that in some of the toads. The young of *draytonii* have thin, soft skins suggesting ancestry in a humid environment; old adults have the dermal covering very rough surfaced and thickened. In *Rana catesbeiana,* native to the humid eastern portion of North America, the skin does not become greatly thickened or roughened with age. *Bufo alvarius,* the toad of the Arizona-California desert, which lives along river courses and around other perennial sources of water, has a smooth skin (evidently an indication of aquaticity) which, however, is thickened, presumably as a check against too great loss of water. It is a *Bufo* which under desert conditions has taken on, in part, the habits and appearance of a *Rana.* The frog of the California foothill streams, *Rana b. boylii,* develops, even at a very early stage, a roughened and thickened type of skin, and the adults are conspicuously pachydermous. The more aquatic member of this group, *sierrae,* and the not distantly related *pretiosa,* which inhabit lakes or perennial streams in high altitudes or more northern latitudes, are smoother and thinner skinned than either *boylii* or *muscosa* of the hot dry foothill regions in central and southern California.

A second response to dry conditions is found in the terrestrial spawning habits of the western species of Plethodontidae. Wilder and Dunn (1920) have advanced the theory that the Plethodonts were originally inhabitants of mountain brooks and that the land-dwelling habit is a secondary development. All of the western species belonging to this group, so far as their habits are known, are strictly terres-

trial in all stages of their existence, and one form, *Aneides lugubris,* conducts its spawning operations in the arboreal habitat of damp holes in oak trees.

In California, no one locality, save perhaps in the extreme northern part of the State along the Oregon boundary, supports more than two species of frogs. Only two ecologic types are represented, a pond type (*aurora*) and a stream type (*boylii*). Farther north, in Oregon, two pond or marsh types are found (*aurora* and *pretiosa*); but the stream type (*boylii*) is not found beyond southwestern Oregon. Possibly the presence of *Ascaphus truei* excludes *Rana boylii* by way of competition in the northern streams. In the eastern states as many as five species of frogs, each with a particular ecologic preference, may be found in one locality (see Wright, 1914). Comparing other groups than the amphibians we find that the fish fauna of the northeastern United States consists of a large number of species, each with a special ecologic preference. In California the fish fauna even of one of our large rivers comprises a relatively small number of species. For example, the total native fresh-water fish fauna of the entire Sacramento basin is about 21 species, whereas 64 species have been recorded from a single eastern lake (Maxinkuckee in Indiana). Among animals inhabiting arid situations in California, the foothill chaparral areas, for example, there is a relatively large population as to species, each of which can be shown to have particular ecologic requirements.

The point here involved is that in the eastern United States, where moisture in the atmosphere is continuously plentiful and where lakes and streams are present at all times of the year, the aquatic and related environments are finely divided ecologically, whereas in interior California (excluding the northwestern humid coast region), where the climate is relatively arid, where the atmosphere is low in relative content of water vapor, where lakes are few and the streams are of intermittent character, the aquatic and related environments show slight diversification. Incidentally, the ecologic niches in the arid territory are finely divided.

It is of course true that the past geological history of a region controls to some extent the diversity of the aquatic fauna, but, even considering this complication, the meager amphibian (and fish) fauna of the west coast is undoubtedly conditioned to a very large degree by the arid nature of the region and the consequent slight diversification of the aquatic environment.

In general, the climatic features of a region may be diagnosed with some degree of success by a study of the amphibian fauna. Ranas develop best in areas well supplied with moisture; Bufos (or their analogues) are in the ascendancy in dry regions. The *Rana* : *Bufo* ratio in the total amphibian population (species × individuals) of a region is an indication of the region's relative moistness or dryness (temperature being excluded).

There are no strictly stream-inhabiting Salientia in the eastern United States. In the west several species are closely related ecologically to stream life, and other species make use of streams in the course of their life-histories. In the eastern states, at least in the northeastern portion of the country where lakes abound, there are numerous forms which dwell principally in ponds or in the marshy tracts adjacent to ponds. The streams of the northeastern states, with the break-up of winter, carry large quantities of broken ice and snow water. High water continues until well into the summer months. The large volume of water transported and the rather low temperature probably make it impossible for an amphibian to receive, in one season, a quantity of heat sufficient to accomplish growth and metamorphosis. But the ponds, as soon as they are free of ice, begin to absorb heat and this, together with the concurrent growth of aquatic micro-vegetation and insects, makes rapid growth possible for the larvae of amphibians which spawn there.

In contrast to the preceding there are no less than five Salientians in the western United States which, for one reason or another, as will be discussed in the chapters on species, are inhabitants of streams. These are *Ascaphus truei, Bufo alvarius, Hyla arenicolor, Rana b. boylii,* and *Rana b. muscosa.* The lake or pond habitat here is used by *Ambystoma californiense, Dicamptodon ensatus, Rana boylii sierrae,* and *Rana aurora draytonii.*

DISTRIBUTION OF AMPHIBIA IN CALIFORNIA

The amphibian fauna of California is found to be widely different from that of eastern North America. Only one or two of the species west of the crest of the Sierra Nevada have any very close affinities with species east of the Great Plains. *Rana pipiens,* the most widely distributed species of frog in North America, reaches the eastern border of the State; it, however, does not enter the real California

region. Several genera (*Dicamptodon, Batrachoseps,* and *Ascaphus*) are restricted to the western half, or less, of the continent. *Aneides* has until recently (Dunn, 1923*a*) been considered a strictly western genus, and I believe strong evidence is necessary to warrant its extension to include an eastern form.

The relationships of the west coast fauna have not been fully investigated as yet. Stejneger (1905*a, b*) has suggested a center of origin for the discoglossid toads in southeastern Asia; Dunn (1923*b*) states that the relationships of *Triturus torosus* are with an Asiatic species rather than with *T. viridescens* of eastern North America. Cope (1889) listed our *Rana aurora* as a subspecies of the Eurasian *agilis* and our *Rana pretiosa* as a subspecies of the Old World *temporaria,* a grouping not without merit. (See also Cope, 1896.) Among birds and mammals there are numerous forms which indicate close faunal affinities of the North Pacific and Northeast Asiatic coasts.

On the other hand, the Californian fauna undoubtedly includes some southern (Sonoran) elements. *Scaphiopus hammondii,* several of our Bufos (*cognatus, punctatus, woodhousii*), and *Hyla arenicolor* are widely distributed in the American southwest and some of these have probably evolved in this region.

The accompanying table indicates in a general way the distribution of the various species of amphibians in California as known at the present time. An attempt was made to define the ranges in terms of life-zones as these zones are currently mapped in California. Some species conform to these zones fairly well, yet there are numerous exceptions, and there are also serious gaps in our knowledge of the extent of range for a number of species, so that an exact mapping by life-zones seems impracticable at the present time.

For example, *Triturus torosus* occupies in southern and central California the Upper Sonoran Zone (and even portions of the Lower Sonoran Zone); in the northwestern part of California it is present in the Upper Sonoran and Transition zones; near South Yolla Bolly Mountain it occurs in territory referable to the Canadian Zone; in the Cascade Mountains of Oregon it has been reported in territory which is also Canadian; and in southeastern Alaska its zonal status is Canadian. In the Sierra Nevada this salamander has not been found above the Upper Sonoran Zone save at Cisco, Placer County; its general exclusion from the Transition may be due in part to the zonal difference in temperature, but I believe lack of suitable environmental conditions is a more potent factor in its absence there.

TABLE SHOWING THE DISTRIBUTION OF AMPHIBIA IN CALIFORNIA

	Northwest Coast	Inner and Central Coast	Southern Coast	Sacto.-San Joaq. valleys	Lower Sierra Nevada	High Sierra Nevada	Modoc Region	Inyo Region	Mohave Desert	Colorado Desert	Coastal Islands
Triturus torosus	x	x	x		x						
Ambystoma californiense		x		x							
Ambystoma macrodactylum							x				
Ambystoma paroticum	x										
Dicamptodon ensatus	x	x									
Batrachoseps attenuatus	x	x	x		x						
Batrachoseps catalinae											x
Batrachoseps major			x								
Batrachoseps pacificus											x
Plethodon elongatus	x										
Ensatina croceater					x						
Ensatina eschscholtzii	x	x	x		x						
Hydromantes platycephala						x					
Aneides ferreus	x										
Aneides flavipunctatus		x									
Aneides lugubris lugubris		x	x		x						
Aneides lugubris farallonensis											x
Ascaphus truei		1									
Scaphiopus hammondii		x	x	x				x			
Bufo alvarius										x	
Bufo boreas boreas	x						x				
Bufo boreas halophilus		x	x	x	x	x					
Bufo canorus						x					
Bufo cognatus cognatus										x	
Bufo cognatus californicus			x								
Bufo punctatus									x		
Bufo woodhousii										x	
Hyla arenicolor			x								
Hyla regilla	x	x	x	x	x	x	x		x		x
Rana aurora aurora	x										
Rana aurora draytonii		x	x		x						
Rana boylii boylii		x			x	2					
Rana boylii muscosa			x								
Rana boylii sierrae						x					
Rana pipiens						?	x			x	
Rana pretiosa pretiosa							x				
Rana pretiosa luteiventris							x				
Rana catesbeiana		i	i	i	i				i		

1, Siskiyou Mountains only.
2, doubtfully Lake Tahoe.
i, introduced.

Hyla regilla, which is suited by various environments, transcends all zonal boundaries. *Aneides lugubris*, which is closely restricted ecologically, is almost strictly confined to the Upper Sonoran Zone where its shelter, the live oak, occurs, and its geographic range does not exceed the range of that tree. *Bufo boreas halophilus* occurs in the Lower and Upper Sonoran zones in the Sacramento and San Joaquin valleys, in the Upper Sonoran Zone in the foothill districts, while in the southern Sierra Nevada it reaches through Transition and Canadian to the Hudsonian Zone. *Rana boylii boylii* in central California inhabits chiefly, if not exclusively, the Upper Sonoran Zone, entering the Transition Zone only locally; in the northwestern humid coast belt it is present abundantly in both Upper Sonoran and Transition; ecologic conditions are favorable to the species in this area but unfavorable in the Transition Zone of the Sierra Nevada.

The territory included in the several distributional areas mentioned in the table is as follows:

Northwestern coast, Del Norte, Humboldt, and northern Mendocino counties.

Inner and central coast, western Siskiyou, Trinity, Lake, Napa, Sonoma, Marin, western Solano, western Alameda, San Francisco, San Mateo, western Santa Clara, and Santa Cruz counties.

Southern coast, the coastal plain of southern California from Ventura County southward to San Diego County and eastward to the margin of the deserts, including the mountain ranges.

Sacramento–San Joaquin valleys, the valley floors, below 400 feet altitude.

Lower Sierra Nevada, the western slope of the range, between 400 and 7000 feet altitude.

High Sierra Nevada, that part of the range above 7000 feet, from Tuolumne County south to Kern County.

Modoc region, northern Sierra Nevada–Cascade system, and adjacent plateau, northward from Lake Tahoe and eastward from vicinity of Mount Shasta.

Inyo region, Mono and Inyo counties.

Mohave Desert, chiefly the desert portion of San Bernardino County.

Colorado Desert, desert portions of Riverside, Imperial, and San Diego counties east of the mountains.

Coastal islands, all of the islands from the Farallones south to San Clemente.

Summarizing the data in the accompanying table, it will be seen that the northwestern humid coast belt includes most of the salamander population, one toad (which is relatively scarce), one hyla, and two frogs.

Middle California, including the foothill and valley regions west of the high Sierra Nevada, has a population of from one to five species of salamanders, one spadefoot, one toad (two in a few places in southern California), one (or two) hylas, and two frogs.

Alpine California (the high central Sierra Nevada) has one salamander, one toad, one hyla, and one frog (of these, all but the hyla being distinct forms).

The southeastern desert fauna has no salamander, four toads, one hyla (only in cañons), and one frog (locally, in rivers).

The California amphibian fauna, so far as the habits and requirements of the species are known at the present time, may be divided as follows with respect to ecologic requirements:

Completely aquatic species:

?Ascaphus truei

Essentially aquatic species, requiring permanent bodies of water, leaving only in the adult condition and then but seldom:

?Ambystoma macrodactylum	*Rana aurora draytonii*
Rana aurora aurora	*Rana catesbeiana* (introduced).

Essentially aquatic species which spawn in streams; the adults live close to streams:

Hyla arenicolor	*Rana boylii muscosa*
Rana boylii boylii	

Species which live in marshy situations close to standing or running water:

?Bufo alvarius	*Rana pretiosa pretiosa*
Rana boylii sierrae	*Rana pretiosa luteiventris*
Rana pipiens	

Species which spend but a short time in the water, the adults being otherwise terrestrial:

	Estimated time in water in egg and larval stages
Ambystoma californiense	3 months or less
Scaphiopus hammondii	5 weeks
Bufo boreas boreas	
Bufo boreas halophilus	4–6 weeks
Bufo canorus	
Bufo cognatus cognatus	
Bufo punctatus	
Bufo woodhousii	
Hyla regilla	6–8 weeks ±

Species with long aquatic larval stage, followed by alternate terrestrial and aquatic stages of varying length:

Triturus torosus	*Dicamptodon ensatus*
?Ambystoma paroticum	

Species entirely terrestrial, eggs deposited in damp situations on land:

Family Plethodontidae (except *Aneides l. lugubris*)

Species terrestrial or arboreal, eggs deposited in damp situations at or above surface of ground:

Aneides lugubris lugubris

NOMENCLATURE

The sequence of species in the following list is exactly that of Stejneger and Barbour (1923) except that *Rana catesbeiana* is placed after the native frogs because it is an introduced species. The nomenclature of the check list cited is followed save where material given in the text indicates the necessity for change. Some readers may raise the objection that an undue number of changes have been made in the scientific names of our familiar species of amphibians, particularly salamanders. To this I would reply that there has been an unusual and pleasing development of interest in the group within the past decade, and reëxamination of many of our species (particularly by Dunn with the advice of Stejneger) has shown the necessity for many changes. The problems in amphibian nomenclature are by no means so complex as some of the contested cases among birds and mammals, in consequence of which we may expect that the present designations will in very large measure be final. The only instances of change in generic names used in the present paper concerning which there is any doubt in my mind are the resurrection of Gray's genus *Ensatina* for the two west-coast Plethodons, *eschscholtzii* and *croceater*, and linkage of "*Spelerpes platycephalus*" with the European *Hydromantes*. Dunn's evidence on these points has not yet been presented in detail. The differences in the arrangement of the vomerine and palatine teeth and in the number of costal folds in the former are considerable and may well merit generic recognition.

The years of publication given for papers in the Journal and Proceedings of the Philadelphia Academy of Natural Sciences are based upon the information contained in the index volume to those series. Yarrow's Checklist is cited as 1883 on the advice of Dr. C. W. Richmond (in letter).

MEASUREMENTS

All dimensions of specimens given in this paper are expressed in millimeters. In order that the measurements of the large number of specimens used might be strictly comparable, a definite method for taking each dimension was decided upon at the beginning of the work. The methods used are described below for the benefit of other workers in the field. All measurements were made by the writer. A vernier caliper reading to 0.1 millimeter was used for taking all measurements except those of the hind feet of toads and frogs and the body and tail lengths of salamanders. The measurements of the mouth parts of Salientian larvae and of the various parts of eggs were made by the use of an ocular micrometer in a microscope at magnifications varying from $\times$ 16 to $\times$ 18.

Unless expressly indicated otherwise, all the measurements given beyond were made on preserved specimens. The dimensions are in most instances somewhat less than they would have been in the living or freshly killed animals. The degree of shrinkage varies in different individuals, the greatest alteration being in the total-length measurements of salamanders and the head-and-body length of toads and frogs. In a few instances where the specimens happened to have been measured when fresh and again after preservation, the exact amount of shrinkage was determined. In some specimens the decrease was less than 2 per cent, in others as much as 10 per cent, the average being about 7 per cent. Specimens distorted in preservation were straightened as well as possible before taking the measurement of total length. Variations in successive readings of such measurements as total length and length of tail may vary as much as 0.5 millimeter on animals over 40 millimeters in length. The shorter measurements can be made with a higher degree of exactitude.

In the tables of measurements given under the several species I have not thought it desirable to average the measurements. Each species of amphibian has a general maximum size toward which it grows, yet the general population of adults within a species does not attain to that narrow compass of variation seen in some species of birds and mammals.

METHODS OF TAKING MEASUREMENTS

CAUDATA

(See fig. G)

Total length, from tip of muzzle to end of tail.

Tail length, from *posterior* margin of anal opening to tip of tail.

Snout to gular fold, taken in straight line from tip of muzzle to center of gular fold.

Greatest width of head, taken transversely over greatest swelling of jaw muscles.

Orbit, longitudinal axis of orbit over anterior and posterior surfaces at juncture of eyelids.

Interorbital space, taken transversely where convex surfaces of orbits approach most closely.

Foreleg, from juncture of leg with body to tip of longest digit, both leg and digits being extended laterally to greatest extent.

Hand, from proximal end of flexed hand (at 'wrist') to tip of longest digit.

Axilla to groin, from posterior surface of fore limb at juncture with body to anterior surface of hind limb.

Hind leg, as for foreleg.

Hind foot, from proximal end of flexed foot ('heel') to tip of longest toe.

SALIENTIA

(See figs. H and I)

Head-and-body, length from tip of muzzle to skin on posterior surface of ischial symphysis.

Length of head, taken in straight line from most anterior part of tip of muzzle to posterior edge of tympanic membrane.

Width of head, taken transversely across angles of jaws.

Orbit, longitudinal axis of orbit over anterior and posterior surfaces at juncture of the two eyelids.

Interorbital space, taken transversely where convex surfaces of orbits approach one another most closely, the position of cranial crests being disregarded.

Forearm, from proximal tip of radio-ulna (olecranon process) to surface of hand, both segments being flexed.

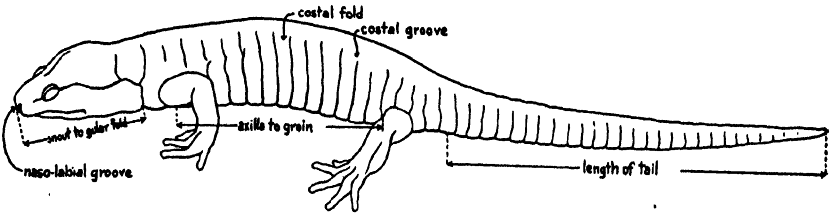
Hand, from proximal end of flexed hand to tip of longest finger.

Femur, from posterior edge of ischial symphysis to distal end of femur, the tibio-fibula being flexed.

Tibia (= tibio-fibula), from convex surface of 'knee' to convex surface of 'heel,' both tibia and tarsus being flexed.

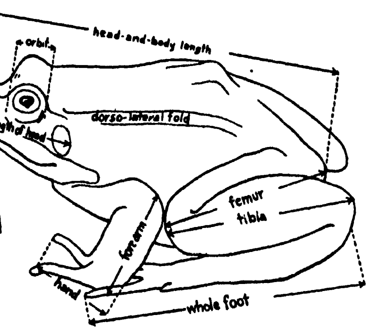
Tarsus, measured over convex surfaces of heel and metatarsus, both tarsus and metatarsus being flexed.

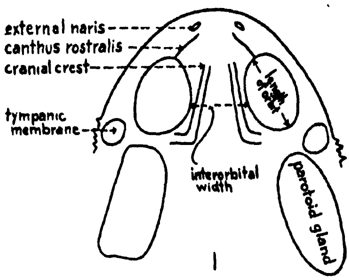
Whole foot, from convex surface of flexed 'heel' along extended and flattened surface of tarsus and foot to tip of longest (fourth) toe.



G

H





I

Fig. G. Outline sketch of *Aneides lugubris lugubris*, showing methods of taking certain measurements and structures mentioned in keys and descriptions.

Fig. H. Outline sketch of *Rana aurora draytonii* showing methods of taking measurements of Salientia.

Fig. I. Outline sketch of head of *Bufo woodhousii* showing location of parts mentioned in key and descriptions.

SECONDARY SEXUAL CHARACTERS

In most species of Salientia in California the sex can be ascertained by external examination alone (see figs. J–L). The sexing of most of the specimens used in the tables of measurements was accomplished in this way, using the following criteria: (1) In *Scaphiopus* and *Bufo* the presence of dark-colored nuptial excrescences (asperities) on the first and second digits of the hand in males. These, while best developed during the breeding season, are present in some individuals captured at other times of year; the darkened vocal sac (when present) is also a usable character. (2) In *Hyla*, the presence of loose, thin, dark-colored skin (vocal sac) on the throat region of males. (3)

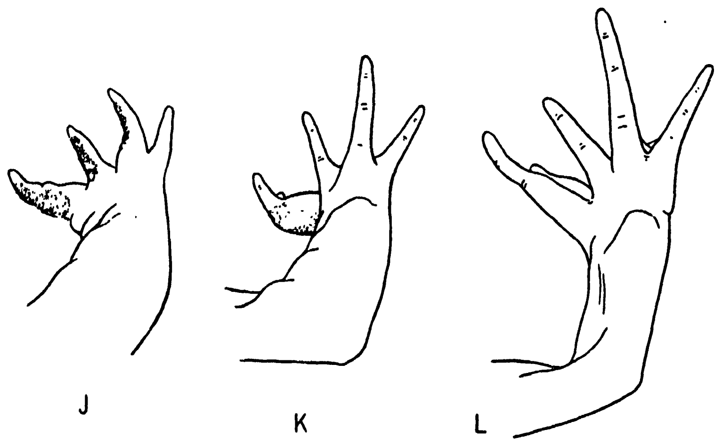


Fig. J. Right fore limb of *Bufo boreas halophilus*, male (no. 5696, M. V. Z.), showing dark-colored 'nuptial' excrescences developed on inner surface of digits. These are absent in females and immature males and reduced in adult males in the non-breeding season.

Figs. K, L. Right fore limb of *Rana aurora draytonii*, male and female (nos. 7151, 7150, M. V. Z.), showing short first digit with enlarged 'nuptial' excrescence and greater development of forearm in male, and elongate form of first digit in female.

In *Rana*, the presence of a nuptial excrescence and the thickened form of first digit on hand in males; the first digit of females is smoothly tapered. Prior to using these criteria, several individuals of each species were sexed by dissection and direct examination of the sex organs. Many females contained eggs in various stages of development or resorption. After laying is completed, the oviducts remain swollen for some time and this condition facilitates determination of 'spent' females. In many of the earlier works on amphibians (includ-

ing Cope's 1889 monograph) differences between the sexes were not considered, although there are important differences in size, surface texture, and measurements in practically all of the western species of Salientia. In the present paper differences between males and females have been indicated wherever found, and the measurements of the two are grouped separately.

In general, adult females average larger in most dimensions, and are rougher surfaced, than males of the same age group.

The Caudata cannot be sexed so readily as the Salientia, therefore the sex of only a few individuals of the former has been determined.

GLOSSARY OF SPECIAL TERMS USED IN DESCRIBING AMPHIBIANS

(See figs. G–O)

Angle of jaw, point where free margins of upper and lower jaws meet.

Canthus rostralis, ridge extending from tip of muzzle to orbit; not present in all species.

Choanae, *see* internal nares.

Commissure, line of juncture of upper and lower jaws.

Costal folds, rounded folds of skin (separated by costal grooves), on sides of body between fore and hind legs in most salamanders; only complete folds, bounded by distinct grooves on both sides, are counted in keys and descriptions.

Cranial crests, paired ridges on dorsal surface of head on interorbital region and between orbit and tympanic membrane in certain toads of Family Bufonidae.

Dorso-lateral folds, two parallel raised ridges of skin along back on certain frogs of genus *Rana*.

Dorsal groove, furrow-like depression along mid-dorsal line of body in some species of salamanders.

Gular fold, transverse fold of skin on ventral surface of body at juncture of throat and body.

Labial teeth, rows of minute slender black epidermal structures on specialized region surrounding mouth on tadpoles of toads and frogs.

Labial papillae, soft rounded lobes or points on mouth region of tadpoles.

Larva, stage in development of an amphibian from time of hatching out of egg capsule until metamorphosis into adult form.

Metacarpal } Metatarsal } tubercles, specialized areas covered by smooth hardened skin on plantar surface of 'hands' and feet of amphibians; metatarsal tubercles sometimes develop as digging 'spades.'

Muzzle, portion of head anterior to orbits.

Nares (external, internal), openings of nasal passages.

Naso-labial groove, small shallow groove connecting nostril with upper lip in salamanders of Family Plethodontidae.

Operculum, thin covering of skin over gills on ventral surface of body in Salientian larvae.

Parasphenoid teeth, broad 'belt' of fine teeth developed on ventral surface of parasphenoid bone in medio-posterior part of roof of mouth in salamanders of Family Plethodontidae.

Parotoid glands, two enlarged distinct glands on dorso-lateral surface of body, one behind each orbit, on toads of Family Bufonidae and on *Ambystoma paroticum.*

Plantar tubercles, *see* metacarpal and metatarsal tubercles.

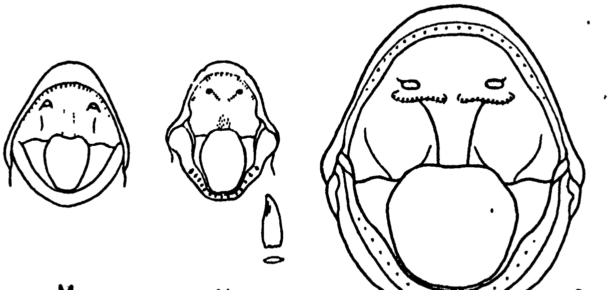
Sacral hump, rounded projection on posterior part of back in frogs of genus *Rana.*

Snout, *see* muzzle.

Spiraculum, opening in opercular membrane of Salientian larvae for exit of water passed over gills.

Tympanic membrane, external ear membrane in toads and frogs.

Vomerine teeth, group of teeth developed on ventral surface of vomers in roof of mouth; form and size characteristic for each species.



M N O

Figs. M, N, O. Opened mouths of *Triturus torosus* (no. 2398, M. V. Z.), *Aneides lugubris lugubris* (no. 2371, M. V. Z.), and *Dicamptodon ensatus* (no. 8573, M. V. Z.), to show differences in teeth in the three families of salamanders inhabiting California. The Salamandridae have no vomerine teeth between the internal nares and only two slender rows of palatosphenoid teeth in the posterior part of the mouth; the Plethodontidae have vomerine teeth developed in relation to the internal nares, and a 'belt' (one or two patches) of parasphenoid teeth in the posterior part of the mouth; the Ambystomidae have well developed vomerine teeth but none posterior to these. The arrangement of vomerine and parasphenoid teeth varies in different species. All our species are provided with maxillary and mandibular teeth. A single mandibular tooth of *Aneides* is shown, enlarged, with the figure of that form.

KEY TO THE ADULTS OF CALIFORNIA AMPHIBIA

PAGE

1. Tail always present; form 'lizard-like'; front and hind legs about equal in development..Order Caudata

 2. No minute groove connecting nostril and upper lip.

  3. Vomero-palatine teeth in two long, nearly parallel lines extending posteriorly far behind internal nares (text fig. M); tongue small, less than half width of mouth at angles of jaws; no large mucous pores around orbit; coloration plain reddish brown and yellow without contrasted markings of any sort; skin rough surfaced in terrestrial individuals (pl. 5, fig. 9)..........Family Salamandridae **Triturus torosus** 44

  3′. Teeth on vomers (between internal nares) in a row extending crosswise of mouth (text fig. O), no teeth in posterior part of mouth; tongue broad, more than half width of mouth at angles of jaws; a series of large mucous pores around and anterior to orbit; coloration often with contrasted markings; skin always very smooth..Family Ambystomidae

PAGE

4. An elongate parotoid gland on each side of neck; no palmar tubercles; costal folds 10; coloration uniform .... **Ambystoma paroticum** 74
4′. No parotoid glands; palmar tubercles usually present; costal folds 11 or 12; coloration not uniform.
   5. Fingers slender, longer than palm; vomerine teeth in four patches; a mid-dorsal stripe of lighter color; total length less than 125 mm.............................. **Ambystoma macrodactylum** 71
   5′. Fingers not longer than palm; vomerine teeth in two patches; total length of breeding adults more than 125 mm.
      6. Body coloration blackish with large distinct spots of yellow (pl. 7, fig. 17); vomerine teeth in a broad forward-directed ∩-shaped pattern; total length under 210 mm.............................. **Ambystoma californiense** 60
      6′. Body coloration 'marbled' with dark brown and black (pl. 7, fig. 14); vomerine teeth in a nearly transverse series (text fig. O); total length up to 287 mm..... **Dicamptodon ensatus** 77

2′. A minute naso-labial groove connecting nostril with upper lip (text fig. G); teeth present on parasphenoid bone in posterior part of mouth (text fig. N).............................. Family Plethodontidae
   7. Limbs much reduced, entire limb scarcely longer than diameter of body, body worm-like, 10 mm. or less in diameter, digits 4, 4, very short (pl. 9, figs. 21, 24).
      8. Costal folds 16 (rarely 15 or 17); habitat San Miguel, Santa Rosa, and Santa Cruz islands .... **Batrachoseps pacificus** 101
      8′. Costal folds 18 to 20.
         9. Costal folds 20[?]; inner finger and inner toe much reduced; habitat Santa Catalina Island.............. **Batrachoseps catalinae** 98
         9′. Costal folds 18 or 19 (rarely 17 or 20); mainland forms.
            10. Costal folds typically 18; under surface of body light yellow; no dark line on side of body.............. **Batrachoseps major** 99
            10′. Costal folds typically 19; under surface of body dark gray or black; a dark line along side of body... **Batrachoseps attenuatus** 89
   7′. Limbs longer, well developed; digits 4, 5.
      11. Teeth on margin of upper jaw inconspicuous; costal folds 10 or 15; digits tapered, not blunt at ends (pl. 9, fig. 22).
         12. Costal folds 15.............. **Plethodon elongatus** 103
         12′. Costal folds 10.
            13. Upper surface of body with large (2–3 mm.) rounded spots of yellow.............. **Ensatina croceater** 104
            13′. Upper surface of body plain colored..... **Ensatina eschscholtzii** 107
      11′. Teeth on front margin of upper jaw projecting distinctly from the skin (text fig. N); costal folds 12; digits all blunt-ended (pl. 9, fig. 20).
         14. Head depressed; tongue freely protrusible, attached by a central pedicel only; digits with webs between bases (text fig. NN); coloration mixed blackish brown and silvery gray.............................. **Hydromantes platycephala** 114
         14′. Temporal region of head swollen; tongue not freely protrusible; color pattern with fine spots or 'marbled'; toes not webbed between bases.
            15. Distal half of tail strongly compressed; coloration black, usually with small rounded white spots.............. **Aneides flavipunctatus** 119

PAGE

15′. Tail rounded or oval throughout.

16. Thumb indistinct; fingers slender; coloration blackish above with numerous irregular light colored markings.. **Aneides ferreus** 117

16′. Thumb distinct; fingers short; coloration brown above, with small rounded yellow spots.

17. Spots fewer; mainland form.......... **Aneides lugubris lugubris** 124

17′. Spots more numerous; habitat South Farallon Island.......... .... **Aneides lugubris farallonensis** 140

1′. Tail absent in adults (a tail-like structure, traversed by cloaca, present in *Ascaphus*); hind legs developed for leaping, much longer and stronger than forelegs... Order Salientia

18. A short tail-like process, not more than ¼ length of body; no tympanic membrane............... ....Family Discoglossidae **Ascaphus truei** 143

18′. No tail or tail-like process in adults; tympanic membrane present.

19. Pupil of eye vertically elliptical; sole of hind foot smooth, without tubercles but with a single black cutting 'spade' on inner margin (pl. 10).......... ....Family Scaphiopodidae **Scaphiopus hammondii** 148

19′. Pupil of eye rounded or horizontally elliptical; sole of hind foot never entirely without low rounded tubercles.

20. An enlarged parotoid gland over shoulder region on each side of back (text fig. I); jaws without teeth.................... Family Bufonidae

21. Cranial crests absent (text fig. OO).

22. Head thick through, skin roughly tubercular; head-and-body length up to 120 mm.

23. Parotoid glands nearly as wide as long, and space between the two about equal to width of one gland (text fig. OO; pl. 17, fig. 51, right) ... . **Bufo canorus** 182

23′. Parotoid glands longer than wide, space between them usually wider than width of one gland.

24. Back either dark and unspotted, or blotched and speckled between the blotches with small, dark dots on the light background; spread of hind foot from end of first toe to tip of fifth toe usually more than 36% of head-and-body length; maximum length 120 mm... . .**Bufo boreas boreas** 167

24′. Back usually spotted or blotched (rarely with dark speckles between the blotches on the light background) and seldom wholly dark; spread of hind foot usually less than 36% of head-and-body length; maximum length 110 mm. .... **Bufo boreas halophilus** 169

22′. Head thin through; skin evenly tubercular; head-and-body length under 75 mm. .... **Bufo punctatus** 192

21′. Cranial crests present on head (text fig. I).

25. Cranial crests curved around eyes; large raised glands present on tibia (pl. 12, fig. 32)... **Bufo alvarius** 163

25′. Cranial crests extending backwards in more or less straight lines, not curved (pl. 11, fig. 31).

26. Parotoid glands short and broad; skin smoother, warts on back smaller, not closely surrounded by black (pl. 11, fig. 31*a*).

PAGE

27. An external cutting tubercle present on hind foot in addition to low tubercles; coloration with green spots .... **Bufo cognatus cognatus** 187
27′. No external cutting tubercle; coloration without green spots .... **Bufo cognatus californicus** 192
26′. Parotoid glands long, obliquely placed and descending on to shoulders; skin rougher, with conspicuously conical, black-ringed warts (pl. 11, fig. 31*b*) .... **Bufo woodhousii** 199
20′. No parotoid glands on shoulders; teeth present on upper jaw.
28. Fingers and toes slender, with round expanded adhesive discs; head-and-body length 50 mm. or less .... Family Hylidae
29. Skin rough, with fine warts, no dark stripe through eye (pl. 13, figs. 37, 38) .... **Hyla arenicolor** 203
29′. Skin smooth, without warts; a dark stripe extending along side of head through eye (pl. 14, figs. 40, 41) .... **Hyla regilla** 215
28′. Fingers and toes without expanded adhesive discs Family Ranidae
30. Dorso-lateral folds very distinct; numerous distinct rounded light-bordered black spots on back strongly contrasted with lighter ground color .... **Rana pipiens** 266
30′. Dorso-lateral folds less distinct or absent; spots on back less distinct or less contrasted.
31. Tympanic membrane prominently outlined, as large or larger than orbit (pl. 18, fig. 53); skin very smooth (pl. 18, fig. 56); head-and-body length of adults up to 175 mm. .... **Rana catesbeiana** 276
31′. Tympanic membrane less prominent, never as large as orbit; skin variable in surface texture; head-and-body length of adults less than 125 mm.
32. Vomerine teeth rudimentary, on two oblique ridges between the internal nares (text figs. Q–S); tympanic region not darker than rest of head; fold along upper lip colored like rest of body, mottled or dark (pl. 12, figs. 34, 36); red never present in coloration of ventral surface.
33. When hind leg is brought forward along body, inside angle of bent tarsus and tibia reaches at least to naris and often beyond end of snout; tympanum covered with many hispid points (pl. 12, fig. 34).
34. A light patch on top of head; a darker area crossing the posterior half of each upper eyelid, merging insensibly into dorsal color behind (pl. 16, fig. 49); head-and-body length under 70 mm .... **Rana boylii boylii** 245
34′. No light patch on top of head; darker areas crossing posterior half of each upper eyelid, when present, contrasting with dorsal coloration (pl. 12, fig. 36); maximum head-and-body length 81 mm. .... **Rana boylii muscosa** 262
33′. When leg is brought forward, inside angle of bent tarsus seldom reaches beyond naris; tympanum smooth or with but a few hispid points; no light patch on top of head (pl. 17, fig. 51, left); head-and-body length reaching 73 mm .... **Rana boylii sierrae** 263

PAGE

32′. Vomerine teeth large, in clusters on ends of indistinct oblique ridges between internal nares (text fig. P); tympanic region darker than rest of head (pl. 15, fig. 46) (except in *pretiosa*); fold along upper lip usually white or lighter than rest of head; red usually present in coloration of ventral surface.

35. When leg is extended forward along body, inside angle of bent tarsus reaches to eye or naris, never beyond.

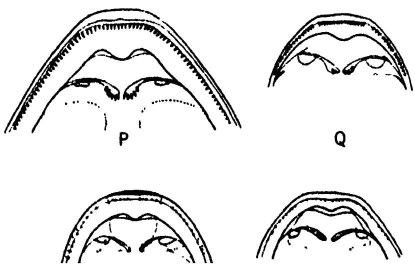
36. Back and top of head, marked with inky, black spots; a small outer metatarsal tubercle........ **Rana pretiosa pretiosa** 270

36′. Back, and top of head, with dark spots not so black as in *pretiosa;* no outer metatarsal tubercle; palmar tubercle small or wanting..**Rana pretiosa luteiventris** 274

35′. Inside angle of bent tarsus when extended forward reaches to or beyond naris; back and top of head without inky spots.

37. Dorso-lateral folds indistinct; skin very smooth and thin; dorsal surface unspotted or with but small dots; size medium; head-and-body length reaching 80 mm........ **Rana aurora aurora** 229

37′. Dorso-lateral folds prominent; skin thick and often slightly roughened; dorsal surface with regularly placed, light-centered dark spots (pl. 15, fig. 46); size large, head-and-body length reaching 115 mm........ **Rana aurora draytonii** 231



Figs. P–S. Mouthparts of California frogs. All natural size.

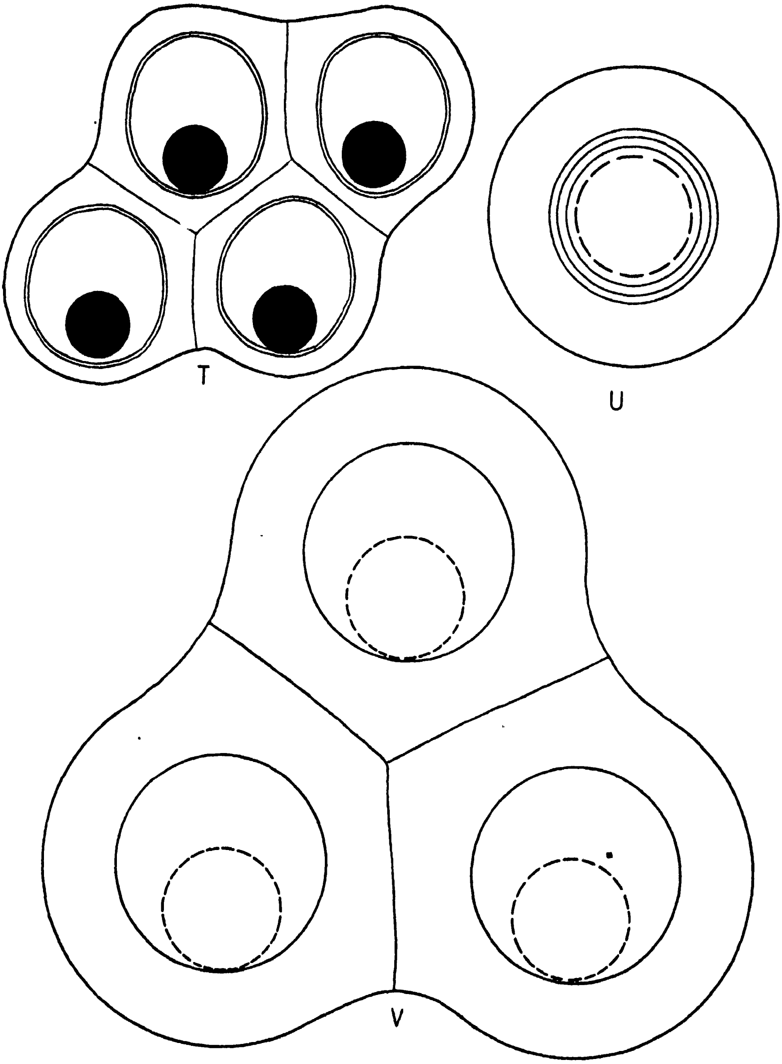
P, *Rana aurora draytonii* (no. 5612, M. V. Z.). Note general large size, prominence of maxillary teeth, and grouping of vomerine teeth between internal nares.

Q, *Rana pretiosa pretiosa* (no. 5566, M. V. Z.). Note similarity to preceding in form and arrangement of teeth, but smaller size, comparing with next two.

R, *Rana boylii sierrae* (no. 3734, M .V. Z.). Note scattering of vomerine teeth.

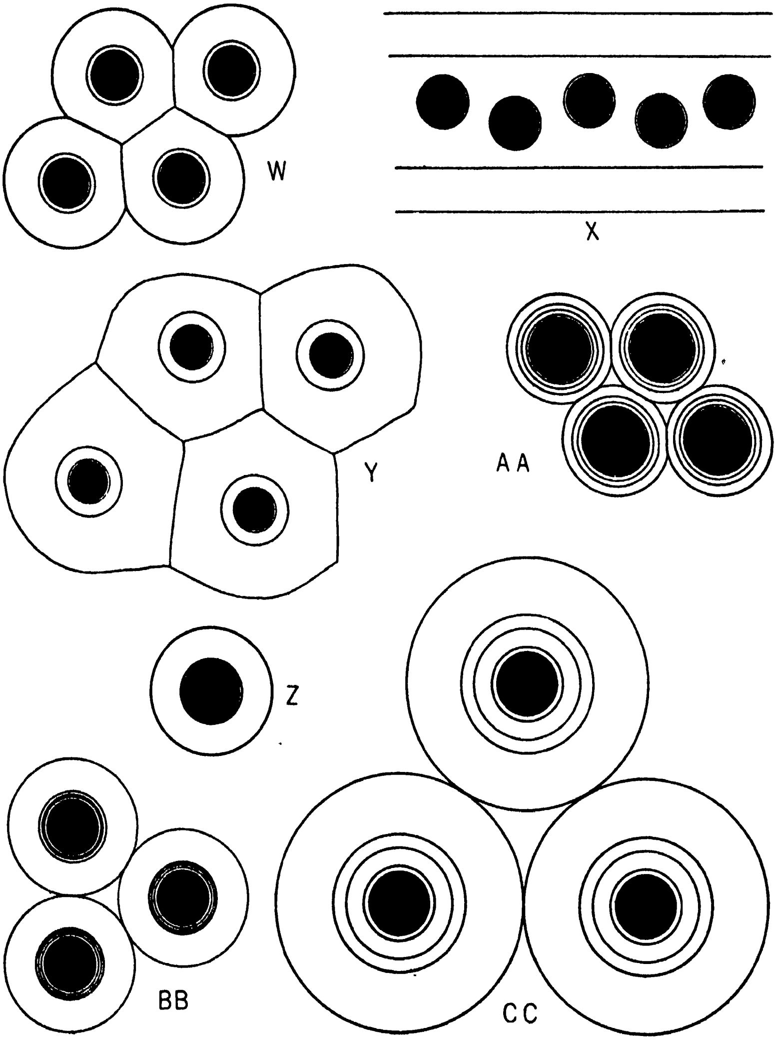
S, *Rana boylii boylii* (no. 6100, M. V. Z.). Note scattering of vomerine teeth, and smaller size of maxillary teeth.

(Figs. Q–S = Figs. 1–3 of Camp, 1917*b*, p. 122.)



Figs. T–V. Diagrammatic figures of eggs and their jelly coats of California amphibians; all 4 times natural size.

T, *Triturus torosus*. U, *Ambystoma californiense*. V, *Dicamptodon ensatus*.



Figs. W–CC. Diagrammatic figures of eggs and their jelly coats of California amphibians; all 4 times natural size.

W, *Scaphiopus hammondii*
X, *Bufo boreas halophilus*
Y, *Hyla regilla*
Z, *Hyla arenicolor*
AA, *Rana boylii boylii*
BB, *Rana pipiens*
CC, *Rana aurora draytonii*

KEY TO THE KNOWN EGGS OF CALIFORNIA AMPHIBIA[1]

PAGE

1. Eggs usually peduncled, deposited out of water, in cavities in logs, under stones or boards at the surface of the ground, in burrows in the ground, or aboveground in cavities in oak trees..........................Family Plethodontidae

 2. Size smaller, outside diameter about 6 mm.; deposited under stones, under or in rotted logs, or in holes in ground; to be found during winter season, December to March......................**Batrachoseps attenuatus** 94

 2'. Size larger, diameter of eggs 6 mm. or more (pl. 9, figs. 22, 23); to be found during summer season, April to September.

  3. Eggs deposited typically aboveground in cavities in oak trees, but also in rotted logs and occasionally on damp ground under boxes; season July and August..**Aneides lugubris lugubris** 135

  3'. Eggs deposited typically at or below surface of ground in damp situations; season April to July.. ....**Aneides flavipunctatus**; **Ensatina eschscholtzii** {112, 123}

1'. Eggs not peduncled, sticky surfaced, deposited in water, in rounded clumps, string-like masses, or singly; usually attached to or twined about vegetation.

 4. Eggs in slender string-like masses, enclosed in a tubular sheath of very clear, soft jelly about 5 mm. in outside diameter; within this a cylinder of jelly in which eggs are arranged in two or three parallel rows; individual eggs 1.65 to 1.70 mm. in diameter, black in color (pl. 14, fig. 43; text fig. X); deposited in ponds or in shallow quiet water at margins of streams, often loosely woven around vegetation................. .... **Bufo boreas halophilus** 178

 4'. Eggs deposited singly or in clumps of not more than four or five.

  5. Outer jelly coat about 10 mm. in diameter; two inner coats close about egg; egg not over 4 mm. in diameter (pl. 8, fig. 18; text fig. U); deposited in shallow rain pools attached to stalks of grass below water surface; to be found only north of Tehachapi Pass................. ....**Ambystoma californiense** 66

  5'. Outer jelly coat, 4.14 to 4.68 mm. in diameter; no inner jelly coat; egg 1.83 to 2.10 mm. in diameter (pl. 13, fig. 39; text fig. Z); deposited in pools of quiet water in granite-bouldered foothill streams and attached to dead vegetation on bottom of pools; to be found only south of Tehachapi Pass..........................**Hyla arenicolor** 210

 4''. Eggs deposited, typically, in soft viscid jelly in masses numbering up to 75 eggs; outer soft jelly coat loose and of varying size, not always readily distinguishable in the water; inner jelly coat, 1.88 to 2.00 mm. in diameter; egg, 1.29 to 1.35 mm. (pl. 14, fig. 42; text fig. Y); deposited in quiet water of permanent or temporary ponds at depths of 100 mm. or less; seldom or never in streams.. ....**Hyla regilla** 225

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[1] Accurate determination of the numbers and dimensions of the jelly coats is best accomplished with the egg mass immersed in water under a low power microscope (15–20 diameters) provided with an ocular micrometer. Oblique transmitted light carefully controlled as to amount is useful in distinguishing the inner jelly coats.

PAGE

4‴. Eggs deposited in grape-like masses, outlines of jelly around each egg distinct on exterior of mass.

6. Egg mass small, cubic contents less than 50 cc., 75 eggs or less in one mass; general form of mass elongate; jelly very soft; two jelly coats around each egg, outer jelly coat, 3.25 to 4.44 mm. in diameter, inner coat, 1.63 to 1.94, egg, 1.47 to 1.62 mm. (pl. 10, fig. 29; text fig. W); egg greenish olive in color; deposited in shallow temporary pools, attached below surface to vertical plant stems........................ **Scaphiopus hammondii** 156

6′. Larger mass, 500 or more eggs in one mass; general form rounded, not elongate; three distinct jelly coats around each egg, individual eggs black above; entire laying of one female usually in one mass.

7. Large mass, cubic contents 1000 cc. or more; outside dimensions of mass 65 x 75 x 100 mm. or more; outermost jelly coat on individual eggs, 7.55 to 9.10 mm., middle coat, 3.94 to 4.93, innermost coat, 3.10 to 4.00; egg, 2.06 to 2.30 (pl. 15, figs. 47, 48; text fig. CC); deposited in quiet water of ponds or in pools at the sides of slow-moving streams................**Rana aurora draytonii** 240

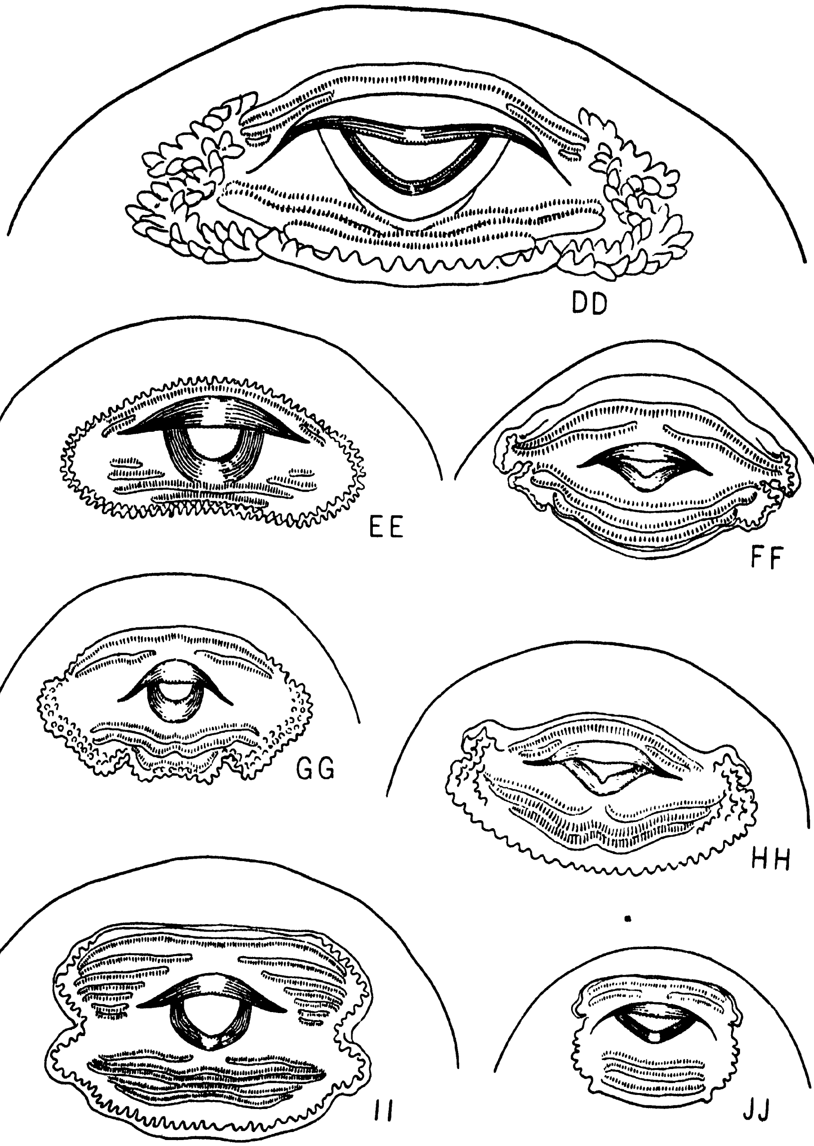
7′. Smaller mass, cubic contents less than 100 cc.; outside dimensions of mass 30 x 45 x 75 mm. or less; outermost jelly coat, 3.88 to 4.47 mm.; middle coat, 2.58 to 3.35; innermost, 2.32 to 2.94; egg, 1.93 to 2.48 (pl. 16, fig. 50; text fig. AA); deposited in water of flowing streams, usually in the current, attached to rocks or pebbles on the bottom..**Rana boylii boylii** 254

7″. Moderate-sized mass, outermost jelly coat, 4.23 to 4.78 mm.; middle coat, 2.22 to 2.72; innermost coat, 2.00 to 2.50; egg, 1.67 to 2.00 (pl. 17, fig. 52; text fig. BB); deposited in ponds or roadside pools..**Rana pipiens** 269

4⁗. Eggs deposited in firm masses, the outlines of individual egg capsules not always showing conspicuously on the exterior; eggs yellowish, not blackish in color.

8. Smaller masses, not more than 25 cc. in volume, outside diameter of mass not more than 30 mm., outer jelly coat around individual eggs about 8 mm. in diameter, egg 2.06 to 2.35 mm. in diameter; vitelline cavity about 4 to 6 mm. in diameter so that egg moves about freely (pl. 5, fig. 11; text fig. T); deposited in ponds or at sides of streams down to 150 mm. below surface of water and attached to vegetation..**Triturus torosus** 54

8′. Larger masses, 150 cc. or more in volume, outside dimensions 60 x 70 x 80 mm. or more, individual jelly capsules about 10 mm. in diameter, vitelline cavity about 5 mm. in diameter; inside of vitelline capsule paved with green algae (pl. 8, fig. 19; text fig. V); deposited in ponds or pools along stream courses attached to vegetation beneath the surface..**Dicamptodon ensatus** 81



Figs. DD–JJ. Mouthparts of mature tadpoles of California Salientia (× 10), at third stage of Dugès (at appearance of hind limb buds).

DD, *Rana catesbeiana*, Standard, Tuolumne County, January 31, 1923.

EE, *Scaphiopus hammondii*, Jenny Lind, Calaveras County, April 9, 1922.

FF, *Bufo boreas halophilus*, Stockton, San Joaquin County, May 22, 1922.

GG, *Hyla regilla*, Lafayette, Contra Costa County, May 22, 1921.

HH, *Rana aurora draytonii*, Arroyo Seco, Los Angeles, April 7, 1923.

II, *Rana boylii boylii*, Camp Taylor, Marin County, August 26, 1922.

JJ, *Bufo punctatus*, 10 mi. ne. of Blythe Junction, San Bernardino County, May 28, 1914.

KEY TO KNOWN LARVAE OF CALIFORNIA AMPHIBIA[3]

PAGE

1. Head broader than and distinct from body; both fore and hind limbs developed at an early stage; external gills present on neck region, not covered (pl. 6, fig.12); mouth parts adapted for swallowing animal (insect) food........Order Caudata
   2. General body coloration chiefly plain yellow with two conspicuous longitudinal stripes of black, one along either side of dorsal fin; size at metamorphosis usually under 60 mm........**Triturus torosus** 46
   2′. Body coloration usually mixed black and yellow, or brown and yellow, but never with lengthwise stripes; vomerine teeth well developed on roof of mouth in U-shaped pattern; size at metamorphosis often more than 60 mm.
      3. Dorsal tail fin extending forward only to above base of tail........**Dicamptodon ensatus** 78
      3′. Dorsal tail fin extending along full length of body to above axillae.
         4. Body coloration mixed light and dark brown with numerous round dots (0.5 mm.) of yellow on lateral and ventral surfaces........**Ambystoma paroticum** 75
         4′. Body coloration yellow and black, without small light dots........**Ambystoma californiense** 61

1′. Head not distinguishable from body, the two fused into a common ovoid mass; gills covered soon after hatching by a thin opercular membrane; limbs not in evidence until late in development (pl. 6, fig. 12; pl. 16, fig. 49); mouth parts adapted for rasping, but not for swallowing large particles........Order Salientia
   5. Spiraculum median, a transverse slit on ventral surface, posterior to 'chin'; upper jaw in form of transverse band of black horny material; lower jaw reduced to a black dot hidden beneath upper; labial teeth in 6/7 (3/10) rows (text fig. KK)........**Ascaphus truei** 144
   5′. Spiraculum on left side of body near middle; upper jaw slightly bowed in outline, lower jaw well developed; labial teeth in 7/5 or fewer rows.
      6. Anus median, emerging in ventral fin.
         7. Body wider posteriorly than anteriorly; eyes well up on top of body (pl. 10, fig. 30); tail fins very broad; ventral surface with bluish or reddish iridescence; total length up to 72 mm.; labial teeth in 2/4 rows, only the first and fifth rows extending across mouth region; mouth region entirely circled with papillae (text fig. EE)........**Scaphiopus hammondii** 149
         7′. Body tapered behind, broadest anteriorly; eyes near sides of body; tail fins narrow (pl. 16, fig. 49, lower two larvae); body solidly blackish; labial teeth in 2/3 rows; papillae only at sides of mouth region........Genus **Bufo**
            8. Size larger, up to 55 mm. total length; lateral margin of mouth region with papillae on both upper and lower halves; lower labial teeth in three graduated rows, lowest row shortest (text fig. FF); not found on deserts of California........**Bufo boreas halophilus** 171

[3]The method of describing the larvae follows that of Boulenger (1891) and Wright (1914).

GENERAL ACCOUNTS OF SPECIES

Triturus torosus (Rathke). Pacific Coast Newt

(Pl. 3, figs. 5, 6; pl. 5, figs. 9–11; pl. 6, figs. 12, 13; text figs. M, T)

Triton torosus Rathke (*in* Eschscholtz, 1833, part 5, pp. 12–14, pl. XXI [fig. 15]). Original description, type from central California.

"*Triton Ermani* Wiegmann (*in* Erman, 1835, Atlas, p. 24": see Wiegmann, 1836, p. 250). Type locality, California.

Salamandra Beecheyi Gray (1839, p. 99, pl. 31 [fig. 3]). Type locality, Monterey.

Notophthalmus torosus, Baird (1850, pp. 284–285). General account.

N[*otophthalmus*]. *torosus*, Baird (1850, pp. 284–285). Locality records.

Triton torosus, Hallowell (1853, p. 238). Habits along Calaveras River.

Taricha lævis Baird and Girard (1853*a*, p. 302). Type locality, San Francisco.

Taricha torosa, Girard (1858, pp. 5–7, pl. 1 [figs. 1–8]). Monograph.

Diemyctylus torosa, Cooper (1868, p. 486). Habits.

Triton torosus, Strauch (1870, p. 51). General account.

Molge torosa, Boulenger (1882*b*, pp. 20–21). General account.

Diemyctylus torosus, Yarrow (1883, pp. 22, 160). Locality records.

Diemyctylus torosus, Cope (1889, pp. 204–206, pls. 36 [fig. 2], 38 [figs. 1–4], 45 [fig. 8], 49 [fig. 3], text fig. 51). Monograph.

Amblystoma rubrum Reid (1895, p. 600). Type locality, Pasadena.

Diemyctylus torosus, Ritter (1897, pp. 73–114, pl. III). Life-history.

Diemyctylus torosus, Ditmars (1906, pp. 2, 11, fig.). Habits in captivity.

Notophthalmus torosus, Grinnell and Camp (1917, pp. 130–131, fig. 1). Range in California.

Notophthalmus torosus, Stejneger and Barbour (1917, p. 7). Range.

Diemyctylus torosus, Fowler and Dunn (1917, p. 28). Locality records.

Triturus torosus, Dunn (1918, p. 450). Locality records.

Notophthalmus torosus, Breder (1923, pp. 73–76, 1 fig.). Habits in captivity.

Triturus torosus, Stejneger and Barbour (1923, p. 3). Range.

Notophthalmus torosus, Grinnell and Storer (1924, p. 651). In foothills of Yosemite region.

Diagnosis.—Size moderate to large among California salamanders, total length up to 225 millimeters (8⅞ inches); no naso-labial groove; skin rough-surfaced in terrestrial individuals, smooth in aquatic males (pl. 5, figs. 9, 10); costal folds absent in terrestrial individuals and aquatic females, sometimes indicated in aquatic males; limbs and digits stout; palatine teeth in two longitudinal rows, posterior to internal nares, the rows nearly meeting anteriorly, separated posteriorly (text fig. M); coloration plain dark brown or black above, orange or yellow beneath, without spots or blotches of any sort.

Comparisons.—Distinguished from all other California salamanders by absence of vomerine teeth immediately behind internal nares on roof of mouth; from Plethodontidae by absence of naso-labial groove and parasphenoid teeth; terrestrial individuals distinguished from all other salamanders by very rough skin, aquatic individuals by irregular development of costal folds.

Description (based on adult individuals listed in tables of measurements).—Form stout, limbs well developed; head pentagonal in outline from above, tip of muzzle truncate; head thin in profile, end of snout rounded; lower jaw overhung by muzzle; external nares close together, terminal, close to margin of upper lip; canthus rostralis moderately developed, its length slightly greater than that of orbit; orbit small, directed latero-anteriorly; interorbital region flat, its width about equal to length of orbit; neck constriction moderate; gular fold imperfectly developed; lower jaw rounded in outline; free portion of upper arm about equaling forearm; palm short; two inconspicuous metacarpal tubercles at sides of palm; digits short, tapered, depressed, in order of decreasing length 3, 2, 4, 1; body stout, swollen at midlength, its cross-section depressed oval in terrestrial individuals, subquadrate in aquatic males; costal folds not in evidence save in aquatic males, then often irregular; hind limbs somewhat stouter than fore limbs, segments short; outer metatarsal tubercle small; toes depressed, tapered, in order of decreasing length 3, 4, 2, 5, 1; cloacal region and tail varying in size according to sex and season; cloacal region but slightly enlarged in terrestrial individuals, greatly swollen in aquatic form, especially males; tail oval in section at base, compressed at tip, with enlarged dorsal and ventral fins in aquatic males during breeding season.

Tongue small, oval in outline, about half width of mouth at angle of jaws, attached along midline to floor of mouth; internal nares small, oval, well in from side of jaw; maxillary teeth small; palatine teeth small, in two slender longitudinal rows, convergent anteriorly, parallel along most of length, divergent posteriorly.

Surfaces varying according to sex and season. Terrestrial individuals rough surfaced on upper and lateral surfaces of head; body and tail, finely areolate, with a raised pointed papilla in each areola; exposed surfaces of limbs similar to body but with smaller papillae; ventral surface of head and body and concealed surfaces of limbs finely areolar, each areola with a minute low papilla; extreme margin of upper lip smooth; plantar surfaces of feet and digits roughened with blunt papillae. Aquatic males smooth surfaced everywhere, with little or no indication of papillae.

General coloration of upper and lateral surfaces of head, body and tail, and exposed surfaces of limbs and feet, plain uniform dark brown, of reddish or blackish hue, sometimes nearly black, especially along sides of body; ventral surface abruptly pale yellow or (less often) orange, of even tint; tips of papillae on ventral surface often blackish; tips of digits in aquatic males, blackish or dark brown; side of swollen cloacal region in male with broad backward stripe of the dark back color encroaching on lighter color of under surface; iris yellow, mottled with black.

A series of nine fresh specimens collected on Paine's Creek, at 600 feet altitude, Tehama County, May 20 and 23, 1924, compared with Ridgway's Color Key (1912) exhibited the following coloration: dorsal surface, aniline black (one) or deep Mars brown (eight); ventral surface varying from scarlet to English red; iris, naphthalene yellow (Grinnell, MS).

Description of larva.—Muzzle truncate oval in outline from above, sloping to rounded tip in profile; external nares terminal; canthus rostralis distinct, about equal to orbit in length; interorbital space greater than length of orbit; sides of head behind orbit parallel; greatest width of head slightly greater than that of body at midlength; costal furrows faint; limbs slenderer than in adult; dorsal fin extending forward to a point between axilla and midpoint of body; ventral fin extends forward nearly to anal opening; gular fold distinct (pl. 6, fig. 12).

MEASUREMENTS OF ADULT SPECIMENS OF *Triturus torosus* FROM CENTRAL AND SOUTHERN CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4992	♀	7 mi. w. Casadero, Sonoma Co.	June 26, 1913	158	82	16.3	15.4	5.7	4.0	21 0	7.5	39 0	22.3	10.4
4986	♀	Gualala, Mendocino Co.	June 30, 1913	165	89	18.7	16.0	5 0	5 0	22 2	8.2	38 0	23.0	11.0
5012	♂	6 mi. n. Willits, Mendocino Co.	Aug. 20, 1913	175	95	20.6	16.5	4.0	...	24.4	9.2	33.5	23.5	12.2
4973	♂	Freestone, Sonoma Co.	June 10, 1913	196	110	19.0	17.6	5.0	5.2	30.0	10.5	36 0	31.8	12.5
4984	♂	7 mi. w. Casadero, Sonoma Co.	June 2, 1913	197	117	21 2	17.0	4 6	4.5	29 2	12.5	31.6	27.7	13.7
4982	♂	7 mi. w. Casadero, Sonoma Co.	June 21, 1913	201	117	21.0	17 2	4.8	6 0	30.6	11.3	34.7	27.2	13 2
4974	♂	Freestone, Sonoma Co.	June 10, 1913	225	128	23.2	20 0	5.6	6 6	29.3	11.5	39.0	30.2	14.3
4474	♀	Sierra Madre, Los Angeles Co.	Apr. 5, 1908	132	65	17.0	16 0	5 6	4 1	24.1	9.0	36.0	24.7	12.0
4475	♀	do	Apr. 5, 1908	133	64	18 0	15 2	5.0	4 5	24.5	9.8	36 0	23.3	11.6
618	♂	do	Apr. 10, 1909	162	90	19 2	17.0	4.4	4.7	26.4	10.0	26 5	26.5	12.7
6855	♂	do	May 30, 1918	164	90	16 8	16.7	5 0	4.2	24.0	11.0	30.0	27.0	13 2
7985	♂	do	May 30, 1918	164	92	18.0	16 0	4.8	4 2	23 0	8.5	27.0	26.2	11.3
4477	♂	do	Apr. 11, 1908	173	97	17.7	16 6	5 4	4 8	27.0	10.0	32.0	27.5	12.0
4478	♂	do	Apr. 25, 1908	180	101	19 2	18.0	5.2	4.5	28.3	10.3	27.0	27.0	13.5

Coloration of upper and lateral surfaces of body and tail, light or dark yellow; a conspicuous dorsolateral line of black on each side extending from posterior portion of head to end of tail; dorsal and ventral fins and sides of body and tail with numerous small dots (1.0 mm. or less) of black; undersurface of body, yellow or white, immaculate.

Remarks on structure and coloration.—The changes in this salamander with respect to age and season are not equaled by those of any other California amphibian (pl. 5, figs. 9, 10). The terrestrial individuals have the skin very rough surfaced, the body is oval in section and the tail oval at base and compressed at tip with little or no suggestion of a fin. The adult males which remain in the water for long periods during the spring breeding period become very smooth surfaced, the papillae of the skin practically disappear, the body becomes nearly quadrangular in section, with conspicuous transverse (costal) folds, and the tail develops a fin both dorsally and ventrally until its height is twice that of the tail in terrestrial individuals. These aquatic males become pale brown on the upper surface and less brightly yellow below, while the lateral area joining the dorsal and ventral surfaces is broadly blackish. The limbs increase in bulk and the tips of all the digits become dark; the cloacal region enlarges until it is half or more the thickness of the body at the groin. The inner surface of the femur on each leg becomes roughened. Females in the water become smoother skinned than when on the land but do not undergo the changes that are indicated for the males. Males which continue in the water after the breeding season become somewhat reduced in bulk and the skin then is more like that of the aquatic females. During the breeding season the two sexes are readily distinguishable by means of the characters described; the sex cannot be determined upon the basis of secondary characters after the animals have left the water for the season.

History.—"*Triton torosus*" was one of the three species of salamanders collected by Dr. Friedrich Eschscholtz during his second visit to California with Captain Otto von Kotzebue in the autumn of 1824. An outline of Eschscholtz' travels within the region is given in the chapter on *Dicamptodon ensatus* (p. 79).

The authorship of the name *torosus* has usually been ascribed to Eschscholtz (Cope, 1889; Ritter, 1897; Stejneger and Barbour, 1917, 1923), but Grinnell and Camp (1917) cite Rathke as the author. That the latter disposition is the correct one is indicated by the fol-

lowing facts: Eschscholtz, upon his return from Kotzebue's second voyage, began, in 1829, the publication of a Zoologischer Atlas in which the species of animals collected on the voyage were described. Eschscholtz is undoubtedly the sole author of the first four parts of the Atlas and hence of the new names proposed therein (for example, *Canis ochropus,* part 3, 1829, pp. 1–2, pl. XI).

Eschscholtz died on May 7, 1831, before the fifth and last part of the Atlas was completed. In a biographical sketch of Eschscholtz, written by Martin Heinrich Rathke, an associate of Eschscholtz at Dorpat, and included in the last part of the Atlas, it is stated that Eschscholtz had written descriptions for certain of the animals intended for inclusion in this part of the work, but that for others only the information set down in his "Tagebuch" (field notes) was available. Rathke undertook to complete the work, adding extensive anatomical descriptions for several species. The brief technical description of *Salamandrina attenuata* (part 5, p. 1) is given with "*E*" as authority, that for *Triton ensatus* (p. 6) is likewise in quotations with Eschscholtz' name appended. Following the few lines describing the external characters there is for each an anatomical description, obviously from Rathke's pen. On pages 12 to 14 there is the description of *Triton torosus* entirely lacking in quotation marks which would ascribe any part of the text there to Eschscholtz, and couched in language similar to that used in the anatomical descriptions added by Rathke to the accounts of the preceding two species. A footnote on page 13 referring to a paper published by Rathke in 1820 is couched in the first person. It seems impossible therefore to do otherwise than ascribe to Rathke authorship for the name *torosus.*

Additional specimens collected by other explorers on the coast of California were described by Wiegmann in 1835 as *Triton Ermani* and by Gray in 1839 as *Salamandra Beecheyi.* In 1849 Skilton described a rough-skinned (terrestrial) individual from Oregon as *Salamandra* (*Triton*) *granulosa,* and in 1853 Baird and Girard gave the name *Taricha lævis* to a smooth-bodied (aquatic) individual collected by Dr. John L. LeConte at San Francisco in February, 1850. Reid in 1895 applied the name *Amblystoma rubrum* to this species in the vicinity of Pasadena.

Range.—*Triturus torosus* is the most widely distributed species of salamander on the Pacific Coast of North America. At the north it has been found in southeastern Alaska at Hassler's Harbor, Revillajigedo [=Revillagigedo] Harbor, and Port Chester (Cope, 1889,

p. 206), and on Admiralty and Dall islands (specimens in Mus. Vert. Zool.); in British Columbia it has been recorded on Vancouver Island, from Fraser River and Chilukiveyuk [= Chilliwack] River (Boulenger, 1882*b*, pp. 20–21), at Bella Coola, Hagensborg, and Ocean Falls (Patch, 1922, p. 75), and at Hatzic and Victoria (Cope, 1893, p. 181); in Washington at Fort Steilacoom, Fort Vancouver (Yarrow, 1883, p. 160), and Tacoma (Cope, *loc. cit.*), near Forks, Clallam County, and at South Bend, Pacific County (specimens in Calif. Acad. Sci.); in Oregon at numerous coastal localities from Astoria, Clatsop County, south to Harbor, Curry County (Calif. Acad. Sci.), and eastward to Portland and Eugene City [= Eugene, Lane County] (Yarrow, *loc. cit.*), and to Drain, Douglas County, and Crater Lake, Klamath County (Calif. Acad. Sci.). Chandler (1918, pp. 7, 11) records the species at Corvallis, and in the Cascade Mountains near Mount Jefferson, Linn County, at an altitude of about 6000 feet. In California this salamander occurs from the Oregon line south certainly to Orange County, and possibly to San Diego (Orcutt, 1885, p. 5; Grinnell and Camp, 1917, pp. 130–131. fig. 1). Eastwardly it ranges to Cisco, Placer County [at 5567 feet] (Grinnell and Camp, *loc. cit.*), to Eldorado County (Cope, 1889, p. 206), to Mokelumne Hill, Calaveras County (Calif. Acad. Sci), to near Coulterville, Mariposa County (Grinnell and Storer, 1924, p. 651), and to "Fresno" [probably the hills east of that place] (Yarrow, *loc. cit.*). In southern California it occurs in the Santa Monica Mountains (Ruthling, 1915, p. 62), in the cañons of the San Gabriel Range as about Sierra Madre (Mus. Vert. Zool.), and in Orange County at Trabuco Cañon (Mus. Vert. Zool.). It apparently is absent from the floor of the Sacramento and San Joaquin valleys. In the Coast Ranges it is present everywhere eastward to the western margin of the Great Valley.

Life-history.—The Pacific Coast Newt, usually called "brown water-dog," is the commonest and best known species of salamander in California. It inhabits every stream cañon where water is to be found during the summer months, and it is frequently to be seen on hill slopes, far removed from water. It is common throughout the foothill districts both in the Coast Ranges and along the Sierra Nevada and in a few places attains to a considerable altitude as on South Yolla Bolly Mountain, Trinity County, at 7000 feet (no. 4997 *et al.*, Mus. Vert. Zool.).

Ritter (1897) has given a rather complete account of the habits and life-history of this salamander. To avoid duplication the present

account will therefore include only the main points in the life-history, emphasizing items lacking or incomplete in the previous paper.

Triturus torosus is a typical "amphibian," spending a part of each year in the water and the rest of the time on land. The eggs are deposited in water, where the larvae grow and metamorphose. Then the young animals quit the water, to return when sexually mature for spawning. Thereafter they enter and leave the water each year at spawning time. The exact division of time between the land and water seems to vary with individuals and locality. In the creeks of the redwood belt in northwestern California some newts are to be found in the water at practically all times of year. In the vicinity of Berkeley and in Mariposa County, to cite only two localities, the animals depart soon after spawning has been completed. The males continue in the water on the average much longer than the females, although the exact period during which any individual remains is unknown. In Thornhill Pond, 3 miles southeast of Berkeley, the male newts are present in numbers for six or eight weeks in the early spring. On one occasion the adults there left the water almost *en masse,* as early as January 26. Ordinarily, a few continue in this particular pond until May. In Blacks Creek, Mariposa County, two adults were seen in a deep pool on May 11 (1919). Adults were common in Papermill Creek, Marin County, on June 1 (1919), and near Inverness, Marin County, several were noted in *Lemna*-covered pools on July 5 (1919). One was seen in a spring on the ridge above Alma, Santa Clara County, on June 23 (1917). In a creek in the redwood belt 10 miles northwest of Ukiah many individuals were seen in the water June 18 to 20 (1922). At Corvallis, Oregon, Chandler (1918, p. 6) states that the adults are aquatic during the summer season, but in October or November they come out on land and in November or December retreat to cavities under logs or stones, coming forth occasionally on warm days. The return to the water may occur as early as the first of January with the males, while with the females it is somewhat later.

Both ponds and creeks are inhabited by the newts during their aquatic existence; when on land they seek shelter during the day under stones, in or under rotted logs, and in the burrows of ground-dwelling mammals. *Torosus* is occasionally to be seen abroad during the daytime, its thickened and roughened skin probably resisting desiccation to a greater degree than the smooth moist body covering of the other species of local salamanders. A majority of the indi-

viduals of *torosus,* however, remain under cover during the daytime, venturing abroad only at night. I do not believe that this restriction of daytime hunting is due to fear of enemies, as *Triturus* is abundantly supplied with dermal poison glands and it has never been reported as being fed upon by any of the local land-dwelling vertebrates whose food habits are known. In this connection see the experiments of Hubbard (1903).

Little is known concerning the habits of the newts during their terrestrial existence. Individuals are occasionally seen walking slowly along paths or clearings in the brush or in the forest, but on the whole a surprisingly small number of terrestrial adults come to human attention in comparison with the large numbers seen in the water. Were *torosus* to breed on land like the local Plethodont salamanders it would probably be much less common in collections. Most of our knowledge of the animals has been obtained while they are engaged in their spawning operations.

The male newts in the vicinity of Berkeley usually begin going to the water in December. The females seem not to enter the water until practically ready to spawn. Active migration of the females toward a spawning place has been witnessed by the writer upon one occasion. On the morning of January 4, 1914, active migration of female newts was in progress at Thornhill Pond. In an area about 5 by 100 feet in extent along a path at right angles to the direction of travel, 13 females were picked up one after another in quick succession; upon reëxamining the area a few minutes later, 3 others had already entered it. Search of the grass-covered ground in the vicinity revealed other females in the ratio of one to every 50 or 75 square feet of ground. The grass on this date was 2 to 3 inches in height. The newts were making their way as best they could, sometimes pushing between the grass blades, again climbing and tumbling awkwardly over the low vegetation. All were definitely headed toward that part of the pond which 12 days later contained a large number of egg masses. One female but slightly over 2 inches in length was found in this migration and going in the same direction as the older ones. The area where these animals were found was shaded by a dense stand of Monterey cypress. Close to the pond 2 other females were found hidden under stones. All of these females exhibited the rough 'terrestrial' form of skin. In the pond on this date were numerous males and a smaller number of females, perhaps in the proportion of 20 to 1.

The waters used by *Triturus* for spawning include creeks, ponds, and reservoirs (pl. 3, figs. 5, 6). The establishment of water storage reservoirs has been a boon to the species in many parts of the State, as these places assure a permanent supply of water, thus permitting large numbers of larvae to complete their metamorphosis.

The breeding season of this newt varies greatly in different parts of its range. At the Thornhill Pond eggs have been found in late December, whereas in southern California spawning has occurred as late as May. The following table gives the available data bearing on spawning.

DATA ON THE SPAWNING OF *Triturus torosus* AT THORNHILL POND, THREE MILES SOUTHEAST OF BERKELEY, ALAMEDA COUNTY, CALIFORNIA

January 15, 1913	many males in water
January 18, 1913	males outnumber females 25 to 1
January 25, 1913	eggs in abundance (none on January 22)
January 26, 1913	all the adults except 3 males had disappeared
January 16, 1914	eggs in abundance
January 31, 1914	various stages from freshly laid eggs to newly hatched larvae; embryos 8–10 mm. long, predominated
February 13, 1914	a few eggs laid during past few days
December 29, 1921	first eggs being deposited; about 15 males and 10 females noted
January 6, 1922	laying in progress; many males and a few more females than on December 29
February 21, 1922	freshly laid eggs last seen on this date
March 14, 1922	two males, no females seen
December 25, 1922	first eggs deposited a day or two previously
January 5, 1923	numbers of eggs and many females engaged in laying; males preponderating
February 1, 1923	bulk of eggs laid prior to this date
February 18, 1923	no females noted during previous two weeks
March 5, 1923	only two males, no females, no larvae
February 2, 1924	first eggs for the season (pond had been examined almost daily during preceding two weeks)

The time at which this species spawns in the creeks of the Coast Ranges is unknown; but on June 18 (1922) there were numerous males with swollen cloacae and many plump-bodied females in a creek 10 miles northwest of Ukiah, Mendocino County. One female taken captive there deposited a few eggs overnight.

The season in southern California is later than in the vicinity of Berkeley. Thus at Sierra Madre on April 3, 1909, males in the water were contending for females, and males with the cloacae swollen were noted on April 11 and 25, 1908, and April 1 and 10, 1909, whereas this condition had disappeared by May of other years (Camp, MS). Females collected at Sierra Madre on April 5, 1908, contained large

DATA ON THE EGGS AND LARVAE OF *Triturus torosus* IN CALIFORNIA

Locality	Date	Stage of development
Vicinity of Berkeley, Alameda Co.	Jan. 22, 1915	Eggs spawned in laboratory
Wildcat Cañon, Contra Costa Co., near Berkeley	Mar. 7, 1920	One egg mass
Strawberry Cañon, Berkeley, Alameda Co.	About March 14, 1914	Eggs reported as being found
San Pablo Creek, Contra Costa Co.	Mar. 14, 1922	Mated pairs numerous; no eggs; females contained eggs ready to lay
San Pablo Creek, Contra Costa Co.	Mar. 27, 1922	Egg masses
Fish Cañon, Los Angeles Co.	Apr. 3, 1921	Eggs found (Hildegarde Howard, MS)
Sierra Madre, Los Angeles Co.	May 7, 1918	Eggs laid this date hatched in captivity June 3 (J. E. Law, MS)
Upper Bailey Cañon, Sierra Madre, Los Angeles Co.	June 1, 1909	Freshly laid eggs (Camp, MS)
Thornhill pond, 3 mi. se. of Berkeley, Alameda Co.	June 21, 1922	One larva 19.5 mm. long
Sierra Madre, Los Angeles Co.	June 22, 1909	Larva about 16 mm. long
Lafayette, Contra Costa Co.	July 18, 1922	Many larvae, about 37 mm. long
San Pablo Creek, near Orinda, Contra Costa Co.	Aug. 7, 1922	Many larvae, 19 to 41 mm. in length
Thornhill pond, 3 mi. se. of Berkeley, Alameda Co.	Aug. 10, 1922	Two larvae, 41 and 46 mm. in length
Strawberry Cañon, Berkeley, Alameda Co.	Sept. 15, 1921	Larva collected this date metamorphosed about Oct. 1; total length 36 mm.

eggs ready for extrusion (Mus. Vert. Zool. nos. 4474, 4475). At Corvallis, Oregon, mating usually begins in February and continues well into summer, copulating pairs being found as late as July 14. Eggs have been found "by the middle of April, and continue to be deposited until the middle of July" (Chandler, 1918, p. 7).

The breeding habits of *torosus* have been described in detail by Ritter (1897) and need only be briefly mentioned here. The males patrol the water and seize the females when the latter enter. The male grasps his mate around the body by both fore and hind legs and his enlarged tail fin serves to carry the two about in the water. The enlarged cloacal region of the male fits down saddle-like over the smaller tail of the female. The method by which transfer of sperm is accomplished has not been discovered, though fertilization is known to be internal as females which have been embraced by males and then isolated lay fertile eggs. After the clasping period the females retire to the margins of the water where they deposit their eggs without further attention from the males.

On one occasion, at the Thornhill Pond (January 17, 1922) a tumbling mass of 20 or more males was noted in the water near the shore. Occasionally individuals left the group and rose to the surface to give off gas bubbles, after which they returned to the group. Females were close about, but so far as could be determined there was none in the mass of males. The cause of this behavior could not be ascertained. Males, in the height of sexual ardor, often grasp at any object near them and the grouping here described may have arisen in response to this reaction.

The eggs of this species are deposited in firm-jellied clumps attached to vegetation in the water (pl. 5, fig. 11). Eggs have been observed in water varying from 25 to 150 millimeters in depth although as a rule they are to be found at depths of 75 to 100 millimeters. The eggs are usually extruded several at a time so that they adhere in clumps, although occasionally single eggs are deposited as with the Eastern Newt (*T. viridescens*). Count of the eggs in 24 typical masses picked up at random in the Thornhill Pond gave the following results: 21, 29, 16, 11, 25, 16, 18, 24, 20, 9, 17, 13, 18, 21, 12, 18, 15, 8, 17, 12, 16, 7, 14, 22, extremes of 7 and 29 and an average of 16.6 eggs per mass. The water displacement of several masses totaling 219 eggs was about 32 cubic centimeters or 0.14 cubic centimeter per egg. The outside diameter of the masses is about 15 millimeters. Each egg is included in a large rounded or oval fluid-filled

cavity with a single layer of gelatinous material outside (text fig. T). The dimensions of the several parts, in millimeters, are as follows:

	Egg diameter	Inside of capsule	Thickness of jelly wall
Minimum	1.88	4.42 x 5.18	0.41
Maximum	2.24	5.12 x 5.58	1.18
Average of 10	2.06	About 4.58 x 5.35	0.63

There is much variation in the color of recently laid eggs. Some are very dark brown on the animal hemisphere (with a light 'polar' spot); others, probably the majority, are light brown above. The lower hemisphere is yellow, sometimes with a greenish cast.

In the vicinity of Corvallis, Oregon, it is reported that the newts deposit their eggs singly (Chandler, *loc. cit.*) as is the habit of *Triturus viridescens* in the eastern states.

Whatever may be the immediate factor which controls the instinctive performance of the reproductive function in this species, its blind operation, in the presence of adverse environmental conditions, often results in a great loss of eggs. At the Thornhill Pond laying may begin just after the first heavy rains in December or early January, the eggs being deposited in the shallow water at the margins. Subsequent rains often fill the pond so that these first eggs are covered to a depth of 300 millimeters (12 inches) or more. This deeper stratum of water often holds much suspended matter, the presence of which decreases the quantity of heat reaching the eggs. Development of the eggs being thus delayed, fungi (*Sporotrichium?*) penetrate the jelly coat, attack, and kill the eggs. On the other hand, eggs deposited later in the season, in shallow water at the pond margin, while receiving a greater quantity of heat, may, by the lowering of the water, be left high and dry and the embryos perish by desiccation (pl. 6, fig. 13).

The eggs of *Triturus torosus* develop much more slowly than the eggs of the Salientia spawned in the same surroundings. In a portion of Thornhill Pond where freshly laid eggs were seen on February 21, 1922, young larvae, just hatched, were found on April 14; thus about 52 days were required for embryonic development. Eggs collected in the field on February 21, 1922, when in the 1-, 2-, and 4-cell stages and kept in the laboratory at an average temperature of 57° F. hatched March 22 to 25, twenty-nine to thirty-two days after laying. Another lot collected on January 5, 1921, was kept in a room where the tem-

perature ranged higher, probably about 65° F.; these began hatching on January 23 and three days later about half of the larvae were out; the time of incubation here was from eighteen to twenty-one days.

A newt larva, at hatching, measured as follows: total length 11.8 mm.; head-and-body 7.35 mm.; thickness of head 1.47 mm.; length of bud of fore limb 1.18 mm.; 'balancer' 1.06 mm.; longest gill filament 1.18 mm.; height over fins at anus 2.06 mm. Camp (MS) notes that the hind limbs appeared on larvae 14 to 16 millimeters long, one week after hatching.

For a short time after hatching the larvae rest on the bottom of the pond, but soon they move about actively and in a few days they avoid observation by darting into the cover of aquatic vegetation whenever frightened. When a month or more of age they are very adept at this and, except in shallow ponds, much careful searching is required in order to find them.

At the Thornhill Pond a larva 19.5 millimeters in total length was found on June 21, 1922, and two, 41 and 46 millimeters respectively, were obtained there on August 10 of the same year. At Lafayette numerous larvae about "1½ inches" (37 mm.) in length were noted in a creek on July 18, 1922. In San Pablo Creek near Orinda, Contra Costa County, larvae were found in abundance on August 7, 1922; they ranged from 19 to 41 millimeters in total length. In 1922 the newts in San Pablo Creek began spawning about March 20.

Larvae of *torosus* have been kept in captivity without metamorphosing for long periods. Ritter (1897, p. 108) mentions one individual which was kept nearly four years and was then preserved to make sure of it for study; Camp (MS) kept some in captivity for a similar length of time, 1908–1912. In the wild, the larvae do not always transform during the same season in which the eggs are laid; thus, four individuals (nos. 4727, 4729–31, Mus. Vert. Zool.) collected in Bailey Cañon at 2500 feet, near Sierra Madre, Los Angeles County, on April 4 and May 11, 1909, measure 52 to 63 millimeters in length, and are nearly but not entirely transformed. They obviously were of the brood of the previous year. At Corvallis, Oregon, Chandler (1918, p. 8) reports that during the middle of summer larvae of two distinct sizes can be found, the smaller up to 21 millimeters in length, the larger averaging about 40 millimeters. In view of the late breeding this author believes that the larvae do not transform until the second summer.

Larval newts collected in Strawberry Cañon, Berkeley, on August 26, 1899, by Dr. L. H. Miller were offered mosquito larvae. The larger individuals (25 mm.) fed voraciously, swallowing the 'wrigglers' head first with a lateral tossing of the (salamander's) head. The insect larvae were too large to be completely swallowed and some of the caudal spines protruded from the mouths of the salamanders. Three days later a salamander larva was seen to seize one of its mates of only slightly smaller size and endeavor to swallow the latter tail first. On another occasion the larvae were fed on chopped pieces of angle-worms which were swallowed with considerable effort; the gorged larvae then moved about very lazily (L. H. Miller, MS).

The size at metamorphosis is small as compared with that of the Ambystomid salamanders. Ritter (1897, pp. 76–77) gives the average length of 9 individuals just metamorphosed as 48 millimeters, and says that the largest he had seen was 60 millimeters in total length. The present writer has had captive individuals as short as 32 millimeters transform, but the transfer from an outdoor pond to a small aquarium may have hastened the metamorphosis at small size. One over-wintered larva from near Sierra Madre is 63 millimeters long.

Following metamorphosis *torosus* is strictly terrestrial. Ritter (1897, pp. 77–78) says that it is absolutely essential that the animals get out of the water at the time of transformation, otherwise they drown. The post-larval growth to sexual maturity occupies at least two years, judging from the size (age) groups at hand.

The following series of specimens indicates the growth of *torosus* after leaving the water:

M. V. Z. No.	Locality	Date	Total length in millimeters
7280	Berkeley, Alameda Co.	Dec. 11, 1919	45.0
7365	North Fork, Madera Co., 3000 ft.	Mar. 8, 1920	46.5
613	Near Sierra Madre, Los Angeles Co.	Mar. 24, 1909	52.0
5013	Freestone, Sonoma Co.	June 12, 1913	52.5
6334	Muir Cañon [Woods], Marin Co.	Sept. 30, 1917	74.0
7628	Lake Leonard, 10 mi. nw. of Ukiah, Mendocino Co.	Oct. 11, 1920	73.0
2402	Muir Woods, Marin Co.	Mar. 5, 1910	78.0
4976	Freestone, Sonoma Co.	June 12, 1913	79.0
4991	7 mi. w. of Cazadero, Sonoma Co.	June 20, 1913	83.0

The smallest breeding individuals measure somewhat more than 100 millimeters in total length. But growth continues for some time after this stage has been reached, as there are two individuals at hand which after preservation measure 225 millimeters in total length.

Several abnormalities have been noted in the rather large number of newts which have passed the writer's notice in the last thirteen years. A larva about 30 millimeters long seen near Berkeley in the autumn of 1911 had a supernumerary hind limb on one side. One adult with bifid tail was seen in a pond near Oakland early in March, 1912, and at least one other of similar character was noted on another occasion. A specimen collected in March, 1912, had a gourd-shaped outgrowth on one side of the throat region.

The building of paved roads in the hills about Berkeley and the frequent use of these roads at night by automobiles results annually in the death of a considerable number of newts in their movements to and from the spawning ponds. The building of a railroad along the north side of Thornhill Pond in 1913 placed a barrier about 30 feet in height which the newts summering on the slopes north of the pond were obliged to cross. In succeeding winters numbers of the animals were killed by passing trains as they attempted to cross the tracks by climbing up on the 'fish-plates.'

Chandler (1918) has indicated the possibility of using this newt in mosquito control work. The species, it seems to me, is adapted to use in some places where the top minnow (*Gambusia affinis*) is unsuited, particularly in the cooler portions of the Pacific coast region where *Gambusia* is less likely to thrive.

The life-history in relation to the environment.—Too little is known about the habits and seasonal program of *Triturus torosus* in places other than the San Francisco Bay region to permit of extensive discussion of probable adaptive features in its seasonal cycle. At and about Berkeley the climatic conditions are so different from those obtaining in other parts of the State that a different adjustment on the part of this salamander evidently occurs. At the Thornhill Pond near Berkeley laying begins soon after the first heavy midwinter rains, as on December 29 (1921) and December 25 (1922). Laying there was suspended during a cold wave at the end of January, 1922, to be resumed with the advent of warmer weather about two weeks later. Laying is practically finished in this pond by the first week of March. It may be that the presence of a permanent pool, with a relatively large drainage basin, ensuring early filling in connection with mild winter temperatures is the basis for early egg deposition.

Data from eggs and larvae in other localities indicate March, April, and May (even June 1) as the time of spawning. Under original conditions ponds were uncommon in the lowlands of California save along the courses of certain of the foothill creeks. These ponds,

like the creeks, were subject to the scouring action of the winter flood waters. Delay in spawning until the subsidence of high water would be of benefit to the newts because their eggs would be less likely to be washed down stream. The situation with respect to the newts which spawn in the streams is much like that described for *Rana boylii boylii* (see p. 259). The newts, however, are able to make use of ponds or reservoirs, which *Rana boylii* seems unable to do. The newts therefore have a wider range of spawning places. The ponds are suitable for egg laying before the streams, and in the absence of competition from other species of salamanders *torosus* could spawn there earlier. Thus *torosus* is able to make use of the habitats of both *Rana boylii* and *Rana draytonii.*

By reason of the long period involved in larval development the newt can continue as a species only in places where there is water throughout the summer season, that is, either in separate ponds or in pools along creeks. The time of metamorphosis seems to be adjusted so that the young ordinarily emerge at or after the beginning of the winter rainy period, making it possible for them to leave the water and migrate without danger of death by desiccation to suitable terrestrial locations for the period of post-larval growth.

The habits of *torosus,* as already pointed out by Ritter (1897), are quite different in many respects from those of *viridescens* of the eastern United States as described by Gage (1891) and others. *Torosus,* structurally, is to be compared with the newts of eastern Asia. It differs from *viridescens* in its larger size, in laying its eggs in masses rather than singly, in the lack of color differences between the recently transformed adult and the older sexually mature animal. The larger size of the adult of *torosus* in contrast with the small size of *viridescens* would seem to be a factor of safety against death by desiccation in the terrestrial stage of the adult. Other things being equal, a small-sized salamander would run greater chance of death from the drying effects of the midsummer temperatures in the California foothills than an animal of larger bulk. The roughened and thickened skin of terrestrial individuals is a factor of aid in the same direction. In its seasonal change from rough to smooth skin, and vice versa, the skin of *torosus* changes from a condition resembling that of the toads of the genus *Bufo* which inhabit the arid portions of the southwest, to a condition like that of the highly aquatic frogs (*Rana aurora, R. pretiosa*) which live in humid surroundings in the northwestern coast district or in high altitudes in the mountains.

Ambystoma californiense Gray. California Tiger Salamander

(Pl. 1, fig. 1; pl. 7, figs. 15–17; pl. 8, fig. 18; text fig. U)

Ambyostoma Californiense Gray (1853, p. 11, pl. 7). Original description, type from Monterey, California.

Ambystonia Californica, Borland (1857, p. 194). Occurrence near Petaluma.

Amblystoma californiense, Baird (1859*b*, pp. 12–13, pl. 30 [figs. 1, 2, doubtfully fig. 3]).

Amblystoma mavortium, Cope (1867, pp. 184–192). Monograph.

Amblystoma mavortium, Strauch (1870, p. 64). Monograph.

Amblystoma tigrinum, Cope (1889, pp. 68–85, pl. 25 [fig. 7], text figs. 12, 13), part. General account.

Amblystoma tigrinum californiense, Cope (1889, pp. 76, 79, 80, 82). Critical account.

Ambystoma tigrinum californiense, Storer (1915, p. 56). Locality records in California.

Amblystoma tigrinum, Grinnell and Camp (1917, p. 138). Range in California.

Ambystoma tigrinum, Dunn (1918, p. 457). Locality records.

Diagnosis.—Size medium among California salamanders, total length up to 207 millimeters (8⅛ inches); skin moderately smooth; ground color black, with numerous large spots of yellow; costal folds usually 11 (rarely 10 or 12); line of vomerine teeth bent forward in a broad U-shape medially, curving laterally to behind internal nares.

Comparisons.—Distinguished from *Dicamptodon ensatus* by smaller size, spotted instead of marbled coloration, 11 instead of 12 costal folds, and by line of vomerine teeth being bent forward between internal nares; from *Ambystoma paroticum* by 11 instead of 10 costal folds, absence of parotoid glands, and by spotted coloration; and from *Ambystoma macrodactylum* by larger size, proportionately shorter digits, spotted pattern of coloration, and vomerine teeth in 2 instead of 4 patches.

Description (based on alcoholic specimens listed in table below).—General form robust throughout; head very thin in profile; outline of snout slightly truncate as viewed from above; canthus rostralis very slightly indicated; top of head almost plane; external nares on line of canthus rostralis; internarial width equal to or greater than interorbital width; distance from naris to orbit greater than diameter of orbit; orbits moderate in size, bulging only slightly above plane of head; interorbital width 1¼ to 1½ times length of orbit; parietal region smoothly rounded to beginning of neck constriction; side of head below orbit smooth; a faint groove from behind orbit to behind commissure of jaw; lower jaw more rounded in outline than upper; gular fold conspicuous; neck constriction slight; body slightly wider than high; limbs stout; free portion of upper arm shorter than forearm; digits four, bluntly tapered, in order of decreasing length 3, 2, 4, 1; longest digit slightly more than length of palm; palm smooth save for two small flat tubercles; costal folds 11 (exceptionally 10 or 12), well indicated in both living and preserved specimens; a shallow mid-dorsal groove in some preserved specimens; hind limb somewhat stouter than

fore limb; digits slightly more slender than those of fore limb, in order of decreasing length 4, 3, 2, 5, 1; two low tubercles on sole of foot, inner one slightly larger; body subquadrate at anal region, beyond which tail is abruptly smaller and compressed to end; dorsal margin of tail with fleshy fin in some individuals; lateral surface of tail near base with numerous vertical grooves; ventral surface of tail flattened near base, compressed distally.

Tongue filling two-thirds or more of width of mouth, exhibiting numerous narrow lengthwise folds; internal nares slightly more separated than external nares; vomerine teeth in two lines, originating laterally behind internal nares, extending forward medially to meet at an angle opposite or slightly forward of anterior border of internal nares. Whole body soft and smooth; mucous pores very abundant.

General ground color (in life) of upper and lateral surfaces of body and tail, chin and throat, and all surfaces of limbs and feet, black; lateral and ventral surfaces of body and of tail (less often dorsal surface as well) with large discrete spots of pale yellow; ventral surface of body, dusky yellow. (In alcohol the dark color fades in varying degree, some specimens becoming bluish black, others pale purplish brown.)

MEASUREMENTS OF ADULT SPECIMENS OF *Ambystoma californiense* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
8206	?	Concord, Contra Costa Co.	Feb. 5, 1921	136[1]	48[1]	21 8	16 5	5 0	6 4	25 0	11 5	40	38.4	13 6
7402	....	Pacheco, Contra Costa Co.	May —, 1920	139	57		14 0	4 3	7 5	24 0	10 0	38	28.0	12.7
5562	♀	Galt, Sacramento Co.	Dec. 31, 1914	163	67	22 4	18.0	4.7	7.0	26 5	11 8	47	31.6	15.0
7266	♀	Concord, Contra Costa Co.	Dec. 24, 1919	182	78	25 0	19 0	4 7	7.2	29 2	12 6	49	32.8	15.5
8240	♀	Ripon, San Joaquin Co.	Apr. 2, 1912	193	91	22 5	21.6	5 0	8 0	29.2	12.6	49	34.0	17.0
8239	♀	Mt. Hamilton, Santa Clara Co.	—— — ——	207	102	26 0	19 3	5 3	7 3	31 7	14.2	47	37.0	16.8

[1] Tail possibly injured.

Description of larva (from living specimens).—Head broad, flat in profile, snout truncate, sides of head nearly parallel posteriorly; greatest width of head about 1½ times greatest diameter of body; no canthus rostralis; orbit situated about twice its diameter from end of snout; interorbital width nearly twice diameter of orbit; body broadest just behind neck region; costal furrows faint; limbs and digits slender; digits and toes slightly exceeding length of palm and sole; dorsal fin high, commencing at posterior margin of head, deeper than body at base of tail, its free margin a smooth slight curve nearly to end of tail; ventral fin beginning just posterior to anus. Gills about equaling head in length, with a double row of filaments along ventral side of each gill (pl. 7, fig. 15).

Vomerine teeth in Ω-shaped pattern, interrupted at midline, extending forward between internal nares, paralleling outline of upper jaw.

Body coloration dull dark green and light yellow, mixed without obvious pattern; dorsal and caudal fins with many large diffuse melanophores; belly semi-iridescent, of a yellowish tinge; legs and feet almost colorless; iris golden yellow, surrounded by black.

History.—The first ascription of a 'tiger' salamander to California occurred in 1853 when Gray described "*Ambyostoma Californiense*" on the basis of a living specimen which was sent by Henry Gurney from Monterey to London, and exhibited in the garden of the London Zoological Society before being preserved in the British Museum. The plate accompanying Gray's article figures the living animal, which is quite like other individuals that I have seen alive in California. Gray's name has generally been relegated to synonymy, but its ultimate standing cannot be decided until a careful monographic study of the species "*tigrinum*" is made, with abundant material from various parts of the country. The present writer inclines to the view that the California population should be considered a distinct form, because it exhibits a general uniformity of color pattern the 'mode' of which is different from that found in other parts of the country; because the life-history here shows points of difference from that indicated for the species elsewhere (see below); because the manner of deposition of the eggs is different from that of "*tigrinum*" elsewhere; and because the local population is isolated from the rest of the species by a rather broad belt of country including a mountain range and a strip of desert.

Range.—*Ambystoma tigrinum,* to which *Ambystoma californiense* is most closely related, is the most widely distributed species of salamander in North America. Its range equals, if not exceeds, that of the ubiquitous Leopard Frog (*Rana pipiens*). At the present time no local races of *A. tigrinum* are recognized, the species being considered the same from the lakes in the Valley of Mexico north to southern Canada (Ottawa), and from Maine to Colorado and Utah. Within this general range there are areas of considerable size in which the species is lacking for want of appropriate local conditions, particularly in the arid portions of the western United States.

Ambystoma californiense has been found at the following localities in California: Petaluma, Sonoma County (Borland, 1857, p. 194); Galt, Sacramento County (Storer, 1915, p. 56); Stockton and Bellota, San Joaquin County, and 4 miles south of Lagrange, Stanislaus County

(Storer, MS); Concord and Pacheco, Contra Costa County (specimens in Mus. Vert. Zool.); Oakland, Alameda County (L. H. Miller, MS); Mayfield and Palo Alto (Dunn, 1918, p. 457), Stanford University (specimens in Calif. Acad. Sci.), and Mount Hamilton, Santa Clara County (Storer, 1915, p. 56); Monterey (Gray, 1853, p. 11); vicinity of San Juan, San Benito County (Calif. Acad. Sci.); Fresno (Cope, 1889, p. 86), and Oleander, Fresno County (Storer, MS); Kings River below Kingsburg in Kings County (J. D. McDonald, MS); and Fort Tejon, Kern County (Cope, 1889, p. 85).

Cope (1867, p. 192), after mentioning the Petaluma material, adds "Numerous specimens from near San Francisco in Mus. Compar. Zoology." Dunn (1918) in listing the material in the Museum of Comparative Zoology, gives only Mayfield and Palo Alto, but mentions a number of specimens. This may be the same material.

Fowler and Dunn in 1917 (p. 8) recorded "*Ambystoma tigrinum*" in California from "McCloud River and spring at 1,500 feet elevation in Coast Range of Humboldt County." The first station is already a locality of record for *Dicamptodon ensatus* and the second is in the heart of the known range of that species; both localities are beyond the geographic limits heretofore known for *Ambystoma tigrinum* [= *californiense*]. In view of the critical nature of these records the writer asked the authors to reëxamine their material which consisted only of larvae. This they have done and they now (March, 1924) determine it to be *Dicamptodon ensatus*.

The foregoing material suggests that the area occupied by *Ambystoma californiense* includes the Great Central Valley and the adjacent foothill districts. The species evidently does not occur in the northwestern humid coast belt (which area is occupied by *Dicamptodon ensatus*), nor in any part of the State south or east of the Tehachapi.

Life-history.—Little is known concerning the habits of the adults of *Ambystoma californiense*. Save during the rainy season the animals are seldom found. Mr. Harry J. Snook states that in and about the city of Stockton, San Joaquin County, adults are occasionally seen in the basements of houses during the winter rainy period. One or two of the animals found in such situations are usually brought each year to his class in biology in the Stockton High School. In the spring, summer, and autumn months nothing is seen of them. Near Ripon, San Joaquin County, on April 2, 1912, an adult female (no. 8240, Mus. Vert. Zool.), was washed up out of a ground squirrel hole in a field which was being irrigated. At Oleander, Fresno County,

about December, 1915, an adult was found some distance underground when a ditch was being dug. At Galt, Sacramento County, on December 31, 1914, a female was found beneath some redwood posts piled on the surface of the ground. These occurrences suggest that the adults take refuge in damp places during the daytime, coming forth at night to forage, and that in the winter they are up near the surface of the ground, whereas in dry weather they probably take refuge in deep burrows.

Examination of the adult animals in the collection of the Museum of Vertebrate Zoology, gives a clue to the probable time of spawning. A female collected near Concord, Contra Costa County, about December 24, 1919, contains numerous ovarian eggs, the largest of which, after preservation in alcohol, are about 2 millimeters in diameter. The specimen collected at Galt, Sacramento County, on December 31, 1914, contains ova of similar size. The female obtained at Ripon, San Joaquin County, on April 2, 1912, has only very small ova. One specimen from Mount Hamilton, Santa Clara County, has the cloacal region greatly swollen, ordinarily a sign of breeding activity, while the oviduct is quite small, suggesting that laying had been completed. This specimen unfortunately bears no date of capture. These data, in connection with the information given below concerning larvae, suggest that egg laying probably occurs regularly in January or February, at the height of the winter rainy season.

In 1924 a special visit was paid to the eastern margin of the Great Valley, in San Joaquin and Calaveras counties, to search for the eggs of this salamander. As stated in the preceding paragraph the information gleaned from examination of adult specimens and the capture of larvae pointed to the peak of the winter rainy period as being the time of spawning. The winter of 1923–24 was very deficient in rainfall and so ordinary calculations were of little value, but it was thought that spawning might occur after the first rain in this period sufficient to establish the usual winter rain pools. Rain to the amount of more than one inch fell in central California on February 6 to 9, and on February 15 numerous pools in western Calaveras and eastern San Joaquin counties were visited and searched for amphibian eggs. The Bellota pool, mentioned below as a regular station for the species, was dry, and in none of the other pools in the near vicinity could any amphibian eggs be found. However, in some similar pools (pl. 1, fig. 1) along the Lodi road, about 2 and 4 miles west of Wallace, in eastern San Joaquin County, eggs were found (pl. 8, fig. 18) which

differed from all known eggs of California amphibia. Upon being taken to the laboratory and hatched, these gave larvae which proved to be those of *Ambystoma californiense.*

The ponds in which these eggs were found, and those in which larvae were collected in 1922 and 1923, were all of the same general type, small pools two acres or less in surface extent, formed in the lowest parts of small drainage basins in the extreme western foothills of the Sierra Nevada. All of these pools are probably ephemeral, as is known to be the case with the Bellota pool, being formed by January or earlier in winters of normal rainfall and becoming dry by early summer. Adjacent to all of the ponds studied there were ground squirrel burrows which the adult salamanders might use as daytime refuges throughout the year, and at the pool two miles west of Wallace there were two rocky outcrops in the interstices of which many salamanders could have found safe retreats.

The water in the ponds west of Wallace was at no place more than 150 millimeters in depth; eggs were found at depths of from 25 to 75 millimeters (estimated), attached to grass stems or stalks of dead weeds under the water surface. The eggs were for the most part deposited singly, though a few doubles and two groups each of three and of four eggs were collected. That this is the regular manner of deposition is indicated by the finding of eggs in two pools, two miles apart, deposited in exactly the same manner.

The outermost jelly coat of the eggs is very soft and evidently viscid at the time of extrusion, since practically all the eggs collected were covered with fine sediment stirred up from the bottom of the pools. This brownish covering tends to obscure the eggs from view above so that careful searching is necessary to discover them. Most of the eggs seen were in an advanced state of development, with well formed embryos bearing gills in which the blood circulation was established. Some of these hatched out in the laboratory on February 17 and the others in the next two or three days. A smaller number had been laid at a later date than the first lot, as the embryos in them were just beginning to elongate on February 15. These hatched in the laboratory on February 28. The eggs of the two age-groups were intermingled. In laying, the females evidently move about much more than is the case with *Triturus torosus* or with any of the common Salientia. It appeared that the eggs of at least three females were represented in those found in the pond two miles west of Wallace.

The eggs of *Ambystoma californiense* are surrounded by three coats of jelly, a soft thick-walled outer coat and two thin, shell-like inner coats, seemingly of slightly greater density, close about the vitelline capsule (fig. U). The dimensions of these parts, in millimeters, are as follows:

	Vitelline capsule	Inner jelly coat	Middle jelly coat	Outer jelly coat
Minimum	3.62	4.25	4.74	8.50
Maximum	5.93	6.36	6.93	12.10
Average of 10	4.57	5.12	5.65	9.87

Eggs in early stages of development would probably measure somewhat less than the foregoing. No cells of green algae were seen within the vitelline capsules of these eggs (compare with account of *Dicamptodon ensatus*, p. 83).

Present information indicates that the eggs of the California Tiger Salamander differ from those of the eastern form (true *tigrinum*) both in form and manner of deposition. Eggs of a number of the salamanders of eastern North America have been described and figured in detail, but no one seems to have described carefully the eggs of this widely distributed species. B. G. Smith (1907, p. 385), in describing the egg masses of *Ambystoma punctatum*, a common eastern species, gives a few suggesions as to the form of eggs of *tigrinum*. He says:

> The eggs [of *A. punctatum*] with their individual gelatinous envelopes, occur in compact bunches, surrounded by a very thick jelly mass. The entire structure is usually of an oval shape, often nearly as large as one's fist. The eggs of *A. tigrinum* are more loosely aggregated in a thinner jelly mass, and the cluster resembles a bunch of grapes. The clusters of eggs of *A. punctatum* are as a rule larger than those of *A. tigrinum*, and the number of eggs in a bunch is usually greater.

Later (B. G. Smith, 1911, p. 19) two masses of *tigrinum* are mentioned containing 53 and 75 eggs respectively. On the other hand, Garman, writing in 1890 (p. 190), stated that *tigrinum* then bred in "thousands" in temporary pools on the Illinois prairies as soon as the snow disappeared in the spring and that "the eggs are [were] laid in large masses attached to dead vegetation."

Engelhardt (1916, pp. 48–51) has described the eggs and larvae of *Ambystoma tigrinum* as seen near Syosset, Long Island, New York (in the spring of 1916?). The basis of identification is not clearly stated. The egg masses were found "at the depth of a foot or more" below the surface, attached to the stalks of dead plants. He says:

The egg masses are rounded oblong or kidney-shaped. The largest measures 3 × 2 inches, the average being about two-thirds of that size. The number of eggs is 30 in the smallest and 110 in the largest mass. . . . the egg masses of *A. triginum* [sic] represent one homogeneous mass of jelly, within which the eggs are distributed irregularly. The eggs measure 3 mm. in diameter, the animal pole being dark brown and the vegetative pole light buff. They are closely surrounded by a clear cell 4 mm. in diameter. I can see no obvious difference between the eggs of this salamander and those of *A. punctatum*, except that the egg masses of the latter species average larger in size and usually contain considerably over 100 eggs.

These eggs were found on April 7. The probable date of deposition was inferred to be not earlier than April 1. Two larvae just at hatching on April 18 measured 13 mm. in total length. An estimate of 20 days for development in the field and laboratory was made. Additional egg masses, deposited after April 7, were found on May 9 (Engelhardt, 1916).

The early embryos of *Ambystoma californiense* are pale yellowish brown in color. As development advances and even before the embryos hatch the 'tiger' markings, characteristic of the later larvae, are in evidence. These are aggregations of melanin at regular intervals along each side of the tail. At the time of hatching the larvae measure about 7 millimeters in head-and-body length and 10.5 millimeters in total length. On the day of hatching they are very active, darting rapidly about and, like the older larvae, avoiding open spaces by taking shelter under any sort of cover afforded. Subsequent development is outlined in the paragraphs following, dealing with material collected in 1922 and 1923.

Acting on general information furnished by Mr. H. J. Snook, the writer made a visit to Stockton and vicinity on April 8 and 9, 1922, in the hope of obtaining some data on the life-history of *Ambystoma californiense*. No material was found then at Stockton, but about 18 miles east of the city, near the settlement of Bellota, a pool was located which contained numerous larvae of this species. These ranged from 47 to 58 millimeters in total length. Several of these larvae were taken to Berkeley and one was reared through the metamorphosis; this change took place about May 8, 1922. Later the same season, about April 24, Mr. Philip N. Baxter of Stockton obtained several larvae, measuring 42 to 47 millimeters in length, in a pool in the western part of the city. One of these which was kept in captivity metamorphosed on June 1 and by July 7 had reached a total length of 60 millimeters. In 1923, I visited the Bellota pool on March 11,

in the hope of observing earlier stages of development, but the season had been enough earlier that the larvae were nearly of the same size as those obtained in 1922, as they measured from 35 to 48 millimeters in length. On March 14, 1923, a pool in the foothills about 4 miles south of Lagrange, Stanislaus County, was found to contain many larvae; a sample lot of these measured 28 to 47 millimeters in total length. On May 14, Mr. Snook obtained many large larvae from a pool in Victory Park, Stockton. Some of these were already undergoing metamorphosis on the date mentioned. Five of the larvae were sent to the writer and four of them metamorphosed within ten days, while the fifth, kept under identical conditions, was still in the larval state on June 26, 1923.

The larval period is short, probably less than four months. Continuance as larvae until a large size is reached would be impossible in most of the ponds in which the species has been observed in California, as these ponds go completely dry in the summer months. Whether the larvae in other localities metamorphose at small size is not known. Osborn in discussing the anatomy of some large "axolotls" from Colorado says that in addition to the large animals which were found in a lake near Crede, "Ordinary larvae of *Amblystoma tigrinum* ranging in length from one to four inches [were present] in the irrigating ditches . . . in the San Luis Valley in the vicinity of Garrison" (Osborn, 1901, p. 888).

The larvae of *Ambystoma californiense* are exceedingly wary. In the pools near Bellota and Lagrange I found that great caution was necessary in order to discover and capture them. When not molested or frightened they will often rest lightly on the bottom in shallow water (from 2 to 8 inches in depth) and in deeper places will remain suspended at this or lesser depths. When resting quietly the gills are extended backward and upward in smooth curves, and the limbs and digits are extended laterally. At the first hint of danger, such as a quick movement on the part of a person, either above or under the surface of the water, the gills are pulled down flat against the body, the limbs are drawn backward along the sides, and the larva, propelled by rapid undulations of its tail and the broad fins attached thereto, darts toward the bottom where it hides under bottom vegetation. The combination of flat head and vertical tail fin joined to a tapered body corresponds to the equipment of a submarine boat, and the rapid course is readily guided by appropriate bending movements of the

proper part of the body. The flat 'shovel' nose makes it readily possible for the larva to work its way under the bottom vegetation.[3]

The life-history in relation to the environment.—The data given above on distribution and life-history show that *Ambystoma californiense* is restricted to a limited area in the central portion of California, namely, the Sacramento–San Joaquin Valley and the central Coast Ranges, and that the seasonal program of the species is arranged to accord closely with the peculiar climatic conditions found there. The environmental conditions for this species are quite different from those obtaining with its close relative, *tigrinum,* in other portions of the continent. It is to be regretted that no ecologic study of *Ambystoma tigrinum* is available for making a comparison with the life-cycle of the California form and for aid in determining the relative importance of the various factors in the environment.

The life-history of *Ambystoma californiense* seems to be closely bound up with the annual cycle of moisture conditions in its habitat. The mean minimal monthly temperature at no time of year goes below the freezing point, therefore temperature can scarcely be said to be a limiting factor. But the supply of pond water, necessary for spawning purposes, *is* limited. Garman (1890, p. 190) says that in Illinois *tigrinum* spawned "*as soon as the snow disappeared,*" [italics mine] which means of course as soon as there was unfrozen water. Here *californiense* has little or no experience with freezing temperatures save for a few hours on occasional nights. Ponds in central California do not remain frozen, but they do dry up because of the low atmospheric humidity, and the lack of rain in the summer months. Hence a species using these ponds must needs advance its spawning to the time when the ponds first become well filled. The autumn rains in central California do not ordinarily result in the establishment of rain pools. Those first rains wet the ground and later, with the advent of additional rain in December and January, ponds are established. Conditions for spawning, so far as *Ambystoma californiense* is concerned, become favorable during January or early in February. Once the eggs are laid, embryonic development is rapid (thus early

[3] A note concerning the method of obtaining these larvae used by the writer may be of service to others. In hunting for the animals the collector is best equipped when provided with dark-colored rubber boots for wading. Taking up a position in the pool and leaning down so that he can see readily into the water he should scan the bottom near clumps of green algae or other aquatic plants. Sudden movements are to be avoided. Larvae can be captured individually by bringing a dip net very slowly under them; then with a quick vertical lift the net and contents is brought above the surface of the water.

embryos collected on February 15 hatched on February 28), so that hatching probably occurs by early February in years of normal rainfall. Meanwhile aquatic vegetation and insects are developing so that by the time the larvae are ready to feed a bounteous supply is available to them. Growth is therefore rapid. Continuance in the larval state, such as occurs with the "axolotls" in the lakes of Colorado and of the Valley of Mexico, would be impossible for the larvae of *A. californiense* in the average pond which dries up by May or June. Metamorphosis therefore takes place in mid-May or early June, and the young salamanders must at once seek shelter in mammal burrows or in such other underground retreats as may offer them protection against desiccation. Subsequent foraging is probably done at night when the relative humidity, particularly in the stratum of air in contact with the ground, is high enough to permit a moist-skinned salamander to venture abroad without danger of desiccation.

The population of *Ambystoma californiense* in California is isolated from the parent stock, "*tigrinum,*" by an area several hundred miles in extent, including the Sierra Nevada and Great Basin. The query arises then as to the probable path by which the *californiense* stock reached California. Two routes seem possible: (1) a southern route, by way of the Mohave and Colorado deserts, at a time when those areas were less arid than they are at present (see chapter on *Hyla arenicolor*, p. 213), and (2) a northeasterly route by way of the northern Great Basin. The southern route may be objected to on the ground that species which reached California by that path, such as *Hyla arenicolor* and *Bufo cognatus* ssp., are to be found at the present time in the region south of Tehachapi. As stated in the paragraph on "Range," *Ambystoma californiense* has never been found south of the southern San Joaquin Valley. Had it arrived through Arizona and southeastern California we would expect to find it represented on the coastal plain of southern California. The northern route, therefore, seems the more probable one. At the present time *tigrinum* is to be found in Colorado, Montana, and Utah. It occurs commonly in some of the high lakes in the Rocky Mountains, as at Lake Solitude, altitude 9,000 feet, Wasatch County, Utah (Van Denburgh, 1915, p. 101), and the lakes on Grand Mesa, altitude 11,000 feet, Mesa County, Colorado (J. D. McDonald, MS). From these localities the species could easily have spread, around the western margin of the Great Basin to the northeasterly part of California. *Tigrinum* also occurs locally in northern Arizona, as on San Francisco

Mountain. So far as known, *A. californiense* does not occur in the alpine lakes of the Sierra Nevada, though many of the lakes would seem to be quite suited to the requirements of the species. It must be recalled, however, that most of the alpine lakes in the Sierra Nevada to the south of Lake Tahoe date only from the last retreat of the ice of the Pleistocene-Recent glaciation. It may well be that prior to the last glacial epoch "*tigrinum*" inhabited a much more extensive range, including both the alpine and lowland portions of California, and that with the advent of glaciers in the Sierra Nevada the species became extinct there but persisted in the lowlands, whence through isolation, the slight change has come about which has developed the form *californiense*.

The present arid condition of the Great Basin is probably a critical factor in restricting *tigrinum* to the mountainous regions along the north, east, and south sides of the Basin. Were this area to experience a moister climate the Tiger Salamander would in all probability spread to many parts of the region unoccupied at present, and it might possibly invade the Sierra Nevada on its eastern flank.

Ambystoma macrodactylum Baird. Long-toed Salamander

Ambystoma macrodactyla Baird (1850, p. 292). Original description; type from Astoria, Oregon.

A[*mbystoma*]. *macrodactylum*, Cooper (1868, p. 486). Range.

Amblystoma macrodactylum, Cope (1889, pp. 95–97, pl. 25 [fig. 6], text fig. 17). General account.

Ambystoma macrodactylum, Van Denburgh (1916, p. 215). Occurrence near Fallen Leaf Lake.

Ambystoma macrodactylum, Grinnell and Camp (1917, pp. 138–139, fig. 1). Range in California.

Ambystoma macrodactylum, Stejneger and Barbour (1917, p. 10; 1923, p. 5). General range.

Diagnosis.—Size moderate among California salamanders, total length 114 millimeters (4½ inches or less); costal folds 11; toes all slender and long; vomerine teeth in broadly Λ-shaped row across mouth mostly behind internal nares, in four separated groups; body coloration uniform dark brown, except for irregular-margined stripe of light color down middle of back.

Comparisons.—Distinguished from Plethodontidae by lack of naso-labial groove and by 11 instead of 10 or 12 or more costal folds; from *Triturus torosus* by slenderer digits, presence of light stripe on back, and presence of four groups of vomerine teeth on roof of mouth; from *Ambystoma paroticum* by lack of parotoid glands, presence of light stripe on back and 11 instead of 10 costal folds; from *Ambystoma californiense* by smaller size, longer digits, striped instead of spotted pattern of coloration, and arrangement of vomerine teeth in angular transverse row instead of U-shaped pattern; from *Dicamptodon*

ensatus by smaller size, 10 instead of 12 costal folds, striped instead of marbled pattern of coloration, slenderer digits, and arrangement of vomerine teeth in 4 instead of 2 groups.

Description (based on 3 specimens from Crater Lake, Oregon).—General form moderate among California salamanders, tail short, digits elongate; head decidedly longer than wide; muzzle oval in outline from above, thin and smoothly rounded at tip in profile; external nares small, laterally placed below canthus rostralis; canthus rostralis distinct though rounded, its length exceeding that of orbit; orbit small; interorbital space slightly convex, about equaling length of orbit; lower jaw evenly rounded; chin and throat flat; neck constriction slight; gular fold distinct, extending up side of neck; fore limb slender; free portion of upper arm slightly longer than forearm; palm practically smooth; digits all slender, decidedly longer than palm, in order of decreasing length 3, 2, 4, 1, inner one well developed; body cylindrical, slightly enlarged at midlength; costal folds 11, not conspicuous; hind limb slightly stouter than fore limb; tibia shorter than free portion of femur; toes long and slender, exceeding length of sole, in order of decreasing length 4, 3, 2, 5, 1; anal region slightly swollen; tail compressed, oval in section at base, thin and fin-like at tip.

Tongue broad, thin, roundedly diamond-shaped in outline, nearly filling floor of mouth and free only at extreme edges; internal nares round, placed well back from tip of muzzle and near to margin of jaw; vomerine teeth in four groups, central pair largest and joined in broadly Λ-shaped pattern between internal nares, two lateral groups smaller and entirely behind internal nares.

Surfaces of body everywhere smooth; a few enlarged mucous pores surrounding orbit, on interorbital space, and on upper lip.

General color (in alcohol) of upper and lateral surfaces of body and tail and exposed surfaces of limbs, dark chocolate brown; broad irregular-margined stripe along mid-dorsal region from neck to end of tail, lead gray; ventral surface dull yellowish brown; lower half of body and limbs everywhere, with many fine dots of whitish.

Patch (1922, pp. 75–76) records the coloration of a specimen 4.55 inches (115 millimeters) in length taken at Watson Lake, 45 miles north of Clinton, British Columbia, September 28, 1918, as follows:

Ground color very dark chocolate brown on sides, slightly lighter on feet, throat, chest and lower surface of tail. Dorsal surface, from muzzle to end of tail, greenish-yellow. This yellow and the brown ground color are about equally present on the muzzle in a spotted arrangement. Entire upper surface of head is yellow, spotted with nine angular areas of brown. The yellow narrows on the shoulders and pelvis, but on the back and tail it has the appearance of paint which has been poured along the vertebral line and allowed to run downward entirely surrounding parts of the ground color, thus forming angular spots, and nearly surrounding others which extend upward into the yellow. There are a few angular yellow spots on the sides. The yellow is crossed by the ground color at two places near the end of the tail. The upper surfaces of the legs and feet are spotted with yellow. The feet, the lower sides, and all under surfaces excepting that of the tail are profusely specked with white. The under surface of the tail is slightly specked with white. Other specimens show variation by having elongated areas of the ground color present along the vertebral line.

The mid-dorsal stripe on the back was grape green in life on a specimen collected at Sawmill Lake, British Columbia.

MEASUREMENTS OF ADULT SPECIMENS OF *Ambystoma macrodactylum* FROM CRATER LAKE, OREGON, COLLECTED JUNE 26, 1918

M. V. Z. No.	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
7166	100	41	13.7	9.5	3.2	3.5	14.5	6.4	30	17.0	9.5
7165	113	49.5	14.5	9.5	3.7	3.2	17.0	7.4	34	18.0	10.7
7164	115	48	13.2	8.7	4.0	3.4	14.6	6.2	28	17.8	8.6

Range.—This salamander occupies a wide extent of territory in the northwestern United States and western British Columbia. In California it has been found near Medicine Lake, Siskiyou County, 6500 feet (Grinnell and Camp, 1917, pp. 138–139) and near Fallen Leaf Lake where three specimens were taken in July, 1915 (Van Denburgh, 1916, p. 215). In Oregon it has been found at Crater Lake (Evermann, 1897, p. 235), and at Fort Klamath and Astoria (Cope, 1889, p. 97). In Washington it has been collected at Cheney, Spokane County, and Prescott, Walla Walla County (specimens in Mus. Vert. Zool.), at Fort Walla Walla (Cope, *loc. cit.*), on Mount Rainier (Van Denburgh, 1912*c*, p. 259), at Hoquam, Chehalis County, and Port Angeles, Clallam County (specimens in Calif. Acad. Sci.), at Semiahmoo, Whatcom County (Cope, *loc. cit.*), and at Springdale, Stevens County (Blanchard, 1921, p. 5). To the east, it is recorded from Fort Custer, Montana (Cope, *loc. cit.*), and in Idaho at Payette Lake, and McCall, Boise County (Van Denburgh and Slevin, 1921*b*, pp. 40–41). Cope (1883, pp. 16–17) under the name *Amblystoma epixanthum* records 4 specimens from near the head of the South Boise River on the south side of the Sawtooth Mountains. In British Columbia this species has been taken at Chiloweyuck [= Chilliwack] Lake (Cope, 1889, p. 97), at Hatzic (Cope, 1893, p. 181), at Watson Lake, Clinton, Bella Coola, and Hagensborg (Patch, 1922, pp. 75–76), and on the Stikine River at Sawmill Lake, 4 miles north of Telegraph Creek (no. 7284, Mus. Vert. Zool.).

Life-history.—Little is known concerning the long-toed salamander. Evermann (1897, p. 235) says that at Crater Lake, Oregon, August 19 to 24, 1896,

It is [was] by far the most abundant and interesting vertebrate occurring at Crater Lake. Our first specimens were found on the shore under Red Cloud Cliff, where we found it to be exceedingly abundant. It was afterward found in considerable numbers along the shore in Eagle Cove, and a few were obtained about Wizard Island. More than a hundred specimens were collected, and many more could have been obtained. The majority of the individuals seen were adults; only 4 or 5 still retaining the external gills were seen. These salamanders were found under the rocks, just above the edge of the water of the Lake. Sometimes as many as a dozen or fifteen were found under a single flat stone.

Ambystoma paroticum Baird. British Columbia Salamander

Amblystoma paroticum Baird *in* Cope (1867, pp. 200–201). Original description, type from Chiloweyuck, Washington Territory [= Chilliwack Lake, British Columbia].

Chondrotus paroticus, Van Denburgh (1916, p. 216). At Requa, Del Norte County, California.

Ambystoma paroticum, Grinnell and Camp (1917, p. 139, fig. 1). Range in California.

Ambystoma paroticum, Stejneger and Barbour (1917, p. 11; 1923, p. 6). General range.

Diagnosis.—Size large, total length up to 179 millimeters (7 inches); body stout; a distinct parotoid gland on each side of neck behind orbit; costal folds 10; digits slender; plantar surfaces of all feet smooth, without tubercles of any sort; vomerine teeth in four groups arranged in a nearly straight line across roof of mouth, posterior to internal nares; coloration plain dark brown above, yellowish brown beneath.

Comparisons.—Distinguished from all other California salamanders by presence of distinct raised parotoid glands on neck region; from Plethodontidae by absence of naso-labial groove and parasphenoid teeth and presence of vomerine teeth; from Salamandridae by presence of vomerine teeth and by smoother body skin; from *Dicamptodon ensatus* by plain instead of marbled pattern of coloration and 10 instead of 12 costal folds; from *Ambystoma californiense* by plain instead of spotted pattern of coloration and 10 instead of 11 or 12 costal folds; from *Ambystoma macrodactylum* by larger size, plain pattern of coloration, and 10 instead of 11 costal folds.

Description (based on adult, no. 29108, Calif. Acad. Sci.).—General form stout, head moderate, limbs well developed; outline of head from above bluntly oval, thin in profile; tip of muzzle flattened between nares, steep in profile; external nares terminal; no canthus rostralis; orbit small, about one-third distance from tip of snout to end of commissure of mouth; eyelid narrow; interorbital space equal to length of orbit; parotoid gland separated slightly from orbit, on side of neck region, the two glands converging posteriorly, each gland about 7 × 14.5 mm., and slightly raised above surrounding surface; angle of jaw behind orbit; deep groove from behind orbit extending ventrally on side of head behind jaw; lower jaw roundedly oval in outline; a swollen gland on side of neck below parotoid on each side, about equaling latter in size; upper and lower glands on each side separated by a deep lateral furrow extending to insertion of foreleg; gular fold narrow, opposite posterior margin of parotoid; free portion of upper arm about equaling forearm; hand slightly longer than forearm; plantar surface of hand entirely smooth, digits long and slender, in order of decreasing length, 3, 2, 4, 1; 10 complete costal folds between axilla and groin; costal grooves sloping dorsoanteriorly; dorsal groove distinct in preserved specimen; hind limb much stouter than fore limb; exposed portion of femur longer than tibia; foot decidedly longer than tibia; plantar surface of foot entirely smooth;

toes slender, tapered, slightly depressed, in order of decreasing length 3, 4, 2, 1, 5; cloacal region slightly swollen; tail compressed oval at base, one-third higher than wide, flattened to thin compressed fin at tip.

Tongue thin and narrow, about one-third (half) width of mouth at angle of jaws, attached almost completely to floor of mouth; internal nares pyriform in shape, well separated and close to sides of upper jaw; vomerine teeth in 4 linear groups in slightly undulating line across entire roof of mouth, slightly posterior to internal nares; maxillary teeth small and numerous.

Surfaces of body rugose with many conspicuous deep pits in skin everywhere on dorsal and lateral surfaces of body and tail; tip of snout, interorbital region, limbs, and feet, and ventral surface of body and tail, smooth; parotoid gland with numerous blunt papillae.

Color (in alcohol) on dorsal and upper lateral surfaces, dark chocolate brown; ventrally, dingy yellowish brown.

Measurements (no. 29108, Calif. Acad. Sci.).—Total length 179 millimeters; length of tail 83; snout to gular fold 23.6; greatest width of head 19.5; orbit 6.6; interorbital space 6.6; elbow to tip of longest finger 23.8; axilla to groin 39; knee to tip of longest toe 27.8; hind foot 16.4.

Description of larva (based on specimens from Fair Oaks, Humboldt County).—General form stout; head elongate, length to behind gills about 1½ times greatest width; tip of muzzle truncate in outline from above; head thick in profile, forehead sloping, muzzle rounded at tip; external nares small, lateral, nearly terminal, below canthus rostralis; anteorbital region about 1½ times length of orbit; interorbital width greater than length of orbit; body deeper than wide, its greatest width about two-thirds that of head; costal folds 10, furrows well developed; limbs and especially digits slender; dorsal fin commencing at posterior margin of head, height moderate, less than that of muscular part of tail at anus; ventral fin beginning immediately posterior to anus; gills short, about equaling length of commissure of mouth; vomerine teeth in Ω-shaped pattern, parallel to margin of upper jaw, and scarcely interrupted at midline.

General coloration (in alcohol) above reddish brown, paling gradually on lower sides to white of under surface; darker portions of body and tail with numerous spots (1 mm.) of white; exposed surfaces of limbs dusky, concealed surfaces white.

History.—Stejneger and Barbour (1923, p. 6) cite Dunn as suggesting that the type of *Siredon gracilis* Baird represents the larva of this species, in which case the name *gracilis* would supplant *paroticum.* With only the figure (Baird, 1859, p. 13, pl. 44 [figs. 2*a*-*e*]) available I am unable to agree to this disposition. *Paroticum* as represented by larval material from California and Washington has parotoid glands developed in the older larvae (one of which is evidently figured by Baird), an unique character which would scarcely

have escaped the attention of Baird, the costal folds are 10, not 11 as in Baird's figure, and there are small white (not black) spots on the ventral surface.

Range.—*Ambystoma paroticum* has been recorded in extreme southern British Columbia on Vancouver Island (Boulenger, 1882*b*, p. 48), at Chilliwack Lake, at the "coal mines" [=Nanaimo], Vancouver Island (Cope, 1889, p. 106), and at Bella Coola and Hagensborg (Patch, 1922, p. 76). In Washington it has been found at Neah Bay, Clallam County, at Semiahmoo, Whatcom County, and on "Puget Sound" (Cope, *loc. cit.*). The California Academy of Sciences has specimens from Quiniault Bay, Chehalis County, and from Mount Rainier, Pierce County (see also Van Denburgh, 1912*c*, p. 259). No records are at hand from Oregon. In California one adult specimen was taken at Requa, Del Norte County, between May 22 and 26, 1911 (Van Denburgh, 1916, p. 216). A series of larvae taken at Fair Oaks, Humboldt County, August 24 to 28, 1910 (nos. 2339–41, 2344–49, Mus. Vert. Zool.), proves to belong to this species and constitutes the southernmost record to date.

Life-history.—Practically nothing is known concerning the life-history of this salamander. The Requa specimen was taken in wet earth under a stump (Van Denburgh, *loc. cit.*). The larvae obtained at Fair Oaks were in a water reservoir. A large series of specimens (nos. 30004 to 30087, Calif. Acad. Sci.) taken on Mount Rainier, Pierce County, Washington, August 14, 1911, contains larvae of various sizes and in various stages of transformation. The largest larva measures 160 millimeters in total length; the smallest metamorphosing animal is but 108 millimeters long. The larvae taken at Fair Oaks, California, measure 74 to 95 millimeters in total length. The latter undoubtedly were from eggs laid at some time during the spring season of the same year.

At Bella Coola, British Columbia (Patch, 1922, p. 76), larval forms were taken in "flood puddles." On June 10, 1918, larvae 44 millimeters in length were collected which had the "dorsal-dermal border" (dorsal fin) extending forward to the base of the skull. Specimens taken August 10 measuring 63 millimeters in length had lost the dermal border and only the scars of the gills remained.

Dicamptodon ensatus (Eschscholtz). Marbled Salamander

(Pl. 1, fig. 2; pl. 7, fig. 14; pl. 8, fig. 19; text figs. O, V)

Triton ensatus Eschscholtz (part 5, 1833, p. 6, pl. 22). Original description, type from central California, possibly near Fort Ross, Sonoma County; followed (pp. 6–12, pl. 22) by anatomical description by Rathke.

Triton ensatus, Baird (1850, p. 288). Monograph.

Amblystoma tenebrosum Baird and Girard (1852*b*, p. 174). Type locality, Oregon.

Xiphonura tenebrosa, Girard (1858, pp. 14–15, pl. 1[figs. 9–17]). General account.

Amblystoma tenebrosum, Cope (1867, pp. 202–204). Monograph.

Dicamptodon ensatus, Strauch (1870, pp. 68–69). *Dicamptodon* new genus, type *Triton ensatus* Eschscholtz.

Amblystoma (?) *tenebrosum*, Cope (1883, p. 24). Larvae at Baird.

Chondrotus tenebrosus, Cope (1887*a*, p. 88; 1889, pp. 111–114, pls. 22, 23, 24 [figs. 1–3], pl. 25 [fig. 3], pl. 48 [figs. 7, 8], text fig. 24). General account.

Triton ensatum, Van Denburgh (1916, p. 221). Nomenclature.

Ambystoma tigrinum, Fowler and Dunn (1917, pp. 8–9). Locality records.

Ambystoma tenebrosum, Stejneger and Barbour (1917, p. 11). Range; footnote on the name *Dicamptodon ensatus*.

Ambystoma ensatum, Grinnell and Camp (1917, p. 139, fig. 1). Range in California.

Ambystoma ensatum, Dunn (1920, pp. 55–56). Structure and nomenclature.

Dicamptodon ensatus, Dunn (1922*a*, pp. 418 *et. seq.*). Structure of sound-transmitting apparatus, and phylogeny.

Dicamptodon ensatus, Stejneger and Barbour (1923, pp. 7–8). Range.

Diagnosis.—Size large, largest of the California salamanders; total length up to 287 millimeters (11¼ inches); skin everywhere smooth; costal folds 12, faintly indicated; limbs heavy; vomerine teeth posterior to internal nares, in nearly transverse row bulging slightly forward at the center where divided; color pattern above 'marbled' with dark brown and black.

Comparisons.—Distinguished from other species of California salamanders by large size (smallest metamorphosed example at hand 122 millimeters in total length) and by marbled pattern of coloration; from *Plethodontidae* by lack of teeth on parasphenoid bone; from Salamandridae by presence of conspicuous teeth on vomers disposed crosswise behind internal nares; from *Ambystoma macrodactylum* by larger size, proportionately shorter digits, and 12 instead of 11 costal folds; from *Ambystoma paroticum* by larger size, absence of conspicuous parotoid glands, and 12 instead of 10 costal folds; from *Ambystoma californiense* by larger size, marbled instead of spotted coloration, straighter rows of vomerine teeth, and 12 instead of 11 costal folds.

Description (based upon no. 8573, Mus. Vert. Zool., in life).—General form robust throughout; head thin in profile, truncate as viewed from above; canthus rostralis rounded; snout above flat, steep

fronted; external nares on sides of snout below canthus rostralis; eyes prominent, bulging high above plane of head; interorbital width slightly greater than length of orbit; parietal region slightly rounded backward to beginning of mid-dorsal groove of back; side of head below eye slanting slightly outward, meeting lower jaw in a smooth curve; a deep groove from behind eye to beyond commissure of jaw, then more faintly to lateral extension of gular fold; between this groove and margin of upper jaw a swollen fold of skin from eye to commissure; an imperfect fold of skin indicated on chin between angles of lower jaw; gular fold deep; neck constriction moderate; upper arm shorter than forearm; palm smooth; digits 4, blunt-ended, in order of decreasing length, 3, 2, 1, 4; body wider than high, slightly swollen at midlength; costal folds 12, the grooves faint and a secondary groove between each two major ones; a shallow mid-dorsal groove from slightly in front of axillae to beginning of tail; hind limb somewhat stouter than fore limb, digits 5, in order of decreasing length, 4, 3, 2, 5, 1; sole entirely smooth, without tubercles of any sort; body subquadrate at anal region, beyond which the tail assumes a compressed form to its end, with slight suggestion of fleshy fin above; lateral surface of tail exhibits a number of vertical grooves; ventral surface of tail flat.

Tongue broad, practically filling lower jaw; vomerine teeth entirely behind internal nares, in two slightly convex transverse rows, bulging forward slightly at center where divided; maxillary teeth numerous and conspicuous.

Entire surface of body soft and smooth, abundantly supplied with closely spaced mucous pores evident to unaided eye; in addition, a finer series of pores may be seen at magnification of 17 to 20 times.

Ground color, Hay's brown on head, near deep brownish drab on body and tail; a 'marbled' or reticulated pattern of blackish markings over ground color everywhere on dorsal surface, and about halfway down sides of body and two-thirds distance down sides of tail, this pattern also appearing on exposed surfaces of limbs; ventral surface without pattern; ground color light cinnamon drab with irregular patches near ivory yellow; vicinity of gular fold pearl gray; soles of feet pinkish; midventral surface of tail light colored like belly; iris deep brown; pupil bluish black (colors from living specimen compared with Ridgway [1912]).

Description of larva (based on forty alcoholic specimens under no. 6342, Mus. Vert. Zool.).—Muzzle truncate, trapezoidal as viewed from above; forehead in profile sloping evenly to end of snout which is quite thin; canthus rostralis slightly indicated; orbit situated more than its diameter from end of snout; interorbital width slightly less than diameter of orbit; greatest width of head slightly more than that of middle of body; a slight mid-dorsal groove; costal furrows faint; limbs and digits proportionately about as in adult; dorsal tail fin extends forward to opposite anterior border of anus; ventral fin stops slightly anterior to midpoint in length of tail (in the older larvae at hand from Fair Oaks [nos. 2342, 2343] the dorsal fin ends midway of the tail).

Vomerine teeth extend forward between internal nares, in broad U-shaped outline, paralleling margin of upper jaw, the two rows nearly meeting in midline anteriorly.

Coloration of upper surface and sides of body and tail, dark reddish brown, with many scattered irregular small spots and fine dots of pale flesh color; undersurface of head and body and midline of tail below, pale flesh color.

MEASUREMENTS OF ADULT SPECIMENS OF *Dicamptodon ensatus* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4841	....	4 mi. w. Sausalito, Marin Co.	Oct. 5, 1913	178	63	31 0	24 0	7 3	8.2	28 8	14.7	48	37.7	16 8
6345	...	Muir Woods, Marin Co.	Dec. 2, 1917	208	84	32 2	26 0	8 1	9 3	32 4	16 6	59	37.2	19.6
8648[1]	♀	Marin Co.	Sept. —, 1903	224	81	38 0	29 0	7 2	8 7	35 0	15 6	60	40.6	22 0
8238	.	Saratoga, Santa Clara Co.	May —, 1913	227	95	33 7	27 6	7 6	9.2	34 5	16 0	54	43.0	22.0
4924	....	Freestone, Sonoma Co.	June 19, 1913	232	87	33 6	28 6	7.5	11.0	32 5	15.0	67	45 5	19.7
4824	.....	Near San Geronimo, Marin Co.	Apr. 23, 1913	247	103	35 5	29 8	7.8	10 7	40 7	16 2	62	48.0	23 0
9211	...	Costen Lake, 10 mi. nw. of Ukiah, Mendocino Co.	Apr. 28, 1923	248	100	40 0	28 7	7.6	8 0	34.7	14 0	64	43 3	19.5
8647	♀	Muir Woods, Marin Co.	Sept. 2, 1912	265	107	43 3	35 8	9 5	13 7	37 3	18 2	65	50.6	25 0
4922	...	6 mi. w. of Inverness, Marin Co.	May 29, 1913	270	110	44 0	34 0	8 6	11 5	40.5	19 4	65	50 2	26 5
8573	..	Muir Woods, Marin Co.	June 13, 1922	271	106	39 2	33 7	8 7	9.6	37 7	16.6	77	50.0	26.5

[1] Lived in captivity for about 7 years.

History.—*Dicamptodon ensatus* first came to the attention of naturalists in 1824 when Dr. Friedrick Eschscholtz, physician to the Russian explorer, Otto von Kotzebue, discovered a specimen in a foothill cañon in central California. Eschscholtz accompanied Kotzebue on both of the latter's voyages around the world and devoted much of his time while in port to collecting natural history specimens. On his second visit to California in September to November, 1824, in company with Kotzebue he visited the Santa Clara Mission, sailed up the Sacramento River as far as the site of the present city of Sacramento, and made a trip from San Francisco to San Rafael Mission, thence overland to Fort Ross, returning by boat to San Francisco. The third journey was made early in October, between the second (or third) and twelfth of the month. It is probable that the "*Triton ensatus*" was obtained at that time, somewhere in the neighborhood of Fort Ross in Sonoma County. Unfortunately the exact locality at which the type specimen was obtained must remain in doubt, for against the

chronology of Eschscholtz' travels as indicated in Kotzebue's narrative (1830, vol. 2), we have Eschscholtz' statement that his specimen was collected in November: "Lebt in Californien, wo das hier beschriebene Exemplar in November an einer Quelle gefunden wurde" (Eschscholtz, 1833, pt. 5, p. 6). Either the latter is a *lapsus calami* for October, or else Eschscholtz made other trips within the range of the species which are not mentioned by Kotzebue. The expedition sailed from San Francisco on November 25, 1824.

This species was subsequently described as "*Amblystoma tenebrosum*" by Baird and Girard (1852*b*) on the basis of a specimen collected by the U. S. Exploring Expedition in "Oregon," even though Baird as early as 1849 was aware of Eschscholtz' species. Girard (1858) included *tenebrosum* in the genus *Xiphonura*. Strauch (1870) founded the genus *Dicamptodon* for Eschscholtz' species, while Cope (1887*a*) established the genus *Chondrotus* for a group of Ambystomids of which *tenebrosus* was made the type species. Cope in his monograph on the Batrachia (1889) treated "*Dicamptodon ensatus*" and "*Amblystoma tenebrosum*" separately. Van Denburgh (1916) suggested that these two names pertained to the same species, and Dunn (1920; 1922*a*) confirmed this suggestion on the basis of anatomical studies.

The description provided by Rathke (*in* Eschscholtz, 1833) is to date the only extensive account of the internal anatomy of the species, Cope's account in 1889 being essentially a description of the external features. No account of the life-history has appeared heretofore.

Range.—At the north, *Dicamptodon ensatus* has been recorded at Sumas Lake (Boulenger, 1882*b*, p. 49) and at "Chilowyuck Lake, Oregon" [= Chilliwack Lake, British Columbia] (Cope, 1889, p. 112). This locality is about five miles north of the Washington–British Columbia boundary. The species is not mentioned in any of the lists of amphibians of British Columbia which are at hand. In Washington it occurs on Puget Sound, and in Oregon at Portland and Astoria (Cope, *loc. cit.*). The California Academy of Sciences has a specimen from Tillamook, Tillamook County, Oregon. In California, *Dicamptodon ensatus* has been found coastwise from Requa, Del Norte County (Calif. Acad. Sci.) south to Felton, Santa Cruz County (Fowler and Dunn, 1917, p. 11). At the north it ranges inland as far as Baird, Shasta County (Townsend, 1887, p. 240), but proceeding southward its eastward limit comes nearer and nearer the coast, as indicated by the following limiting records: Allen Springs, Lake County (Grinnell

and Camp, 1917, p. 139), Saint Helena, Napa County, and Agua Caliente, Sonoma County (Calif. Acad. Sci.). South of the Golden Gate it is confined to a narrow coastwise strip nowhere more than fifteen miles in width. Dunn (1918) has recently recorded the species from "Berkeley." I have never found or known of specimens being found on the east side of San Francisco Bay, and I think it probable that the specimens in the Museum of Comparative Zoology which formed the basis of Dunn's record were collected elsewhere, possibly in Marin County, and later shipped from Berkeley.

Life-history.—In a small body of water 10 miles northwest of Ukiah, Mendocino County, known locally as Costen Lake (pl. 1, fig. 2), situated in a rather deep cañon in the redwood forest, I found, on June 18, 1922, some large jelly masses, which, by reason of their size and location, I believed to be the egg capsules of this species. All the eggs had developed and the larvae had hatched out. These jelly masses were firmly attached to twigs of brush which had fallen into the water and the different masses were from 12 to 30 inches below the lake surface. At the time of my visit, the water at this particular spot was brilliantly clear, though most of the lake elsewhere was covered with a dense growth of duckweed (*Lemna* sp.) and other surface plants. The individual jelly masses were on the average about 75 millimeters in diameter. The largest one recovered measured about $75 \times 75 \times 100$ millimeters. The jelly was firmer than that which surrounds the eggs of any of the California Salientia, resembling that in the egg mass of *Triturus torosus*. In the largest of the jelly masses, there were upward of 25 capsules from which larvae had hatched out.

Various portions of the lake were then searched for larvae, but only two were found. One of these was fully 150 millimeters in total length, with gills still in evidence; it was walking on the bottom of the lake in water about 4 feet deep, and within 50 feet of the place where the jelly masses were found. The other larva was discovered while searching the opposite end of the lake where a cold mountain stream entered and where there was a dense growth of water cress. This larva was 49 millimeters in total length. Young trout of about the same length were in the creek. I was told by people in the neighborhood that the large 'gray' larvae are sometimes seen in the deeper pools of the creeks in the cañon bottoms nearby.

At my request, Miss Una Boyle, whose summer home is near Costen Lake, searched the water of the lake late in the spring of 1923 and early in 1924 for egg masses of this salamander. In 1923 she found

four masses, advanced in development, on April 28. These were forwarded at once to Berkeley and arrived in good condition for study on the day following. In 1924 three masses, with early embryos, were found on or just prior to February 20. These were at once preserved in formalin and subsequently shipped to the writer.

In the 1923 material the embryos in one egg mass had not begun to hatch, in a second some still remained in their capsules, while practically all were out in the remaining two masses when received at Berkeley. Some had evidently emerged while en route. The embryos in the first mentioned mass began hatching on April 29. The embryos in the 1924 material were only about 5 millimeters in length when preserved. Egg deposition in the latter case had in all probability occurred prior to the middle of February. The two seasons of 1923 and 1924 were so different in character as to make it impossible to say whether the two lots of material represent the two ends of the normal seasonal program of *Dicamptodon*. I am inclined to believe that spawning occurs during March of normal years and that the 1924 material was deposited fully a month earlier than usual.

The following table gives the measurements of these egg masses.

Date collected	Weight in grams	Volume in cubic centimeters	Approximate outside dimensions in millimeters
April 28, 1923	304	290	110 x 70 x 70
April 28, 1923	286	280	110 x 70 x 70
April 28, 1923	214	220	70 x 75 x 65
April 28, 1923	184	180	80 x 70 x 60
About Feb. 20, 1924	....	230	80 x 60 x 60
About Feb. 20, 1924	....	240	80 x 65 x 55
About Feb. 20, 1924	....	155	70 x 70 x 45

The individual capsules in which the embryos develop are 6.5 to 7.0 millimeters in diameter in the younger (1924) material and about 10 millimeters in the 1923 masses. As with egg masses of other species, the size of the mass increases as development proceeds. More space is thus afforded for the embryos as they grow in length.

There seems to be only one layer of jelly surrounding each egg, and this, in masses advanced in development, is about 2.5 millimeters thick around each capsule. A complete mass is evidently composed of separate egg capsules, which, upon being laid in groups, absorb water and adhere to each other so closely as to defy subsequent separation (pl. 8, fig. 19; text fig. V).

A most curious characteristic of the egg mass of this amphibian is that the inside of each egg capsule is lined with a coating of small rounded green algae, of sufficient density to be seen easily with the unaided eye. This green coating was observed in the empty egg capsules of the 1922 material when they were found in the lake, but no particular attention was paid to it at the time, since an easy path of entrance was afforded in the openings which the embryos had made at emergence. Upon showing the jelly masses to Dr. J. S. Kingsley, he informed me that some years ago Dr. Fred D. Lambert of Tufts College had made some studies on the similar algal lining which occurs in the egg capsules of a species of *Ambystoma* [*punctatum?*] in Massachusetts and that Lambert had established a new genus for it. Efforts to obtain information concerning the alga from Dr. Lambert have been unavailing. It was with some interest that the same sort of an algal coating was found in the egg masses collected in 1923 and 1924 *before the larvae had emerged.* The algae form a close lining for the entire wall of the capsule. Individually they are spherical or nearly so, with a clear outer wall, the interior being closely packed with greenish granules. In size they range from .011 to .030 millimeters in diameter.

After the larvae have hatched out, the inner lining of the capsule, with its pavement of alga cells, can be removed in one piece, showing that the algae are attached to a lining membrane. None of the alga cells seems to be free in the egg capsule. Professor N. L. Gardner kept some of this material under observation during the summer of 1923 but was unable to determine its systematic position.

Two interesting lines of speculation are aroused by the presence of this alga in the egg capsules of the salamander: (1) how does the alga gain entrance, and (2) what is its function. Appropriate observation would probably clear up the first point, though the problem would require that an investigator be in the field just prior to the time of egg deposition and that an adequate supply of adult animals be available for dissection and for observation of the act of spawning.

Fertilization in salamanders has been found to be internal so far as the subject has been investigated. Kingsbury (1895, pp. 261–304) has ascertained that in a number of genera of salamanders of eastern North America, including *Ambystoma* (to which *Dicamptodon* is closely related), there is in the cloaca of the female a *receptaculum seminis* (one or more) in which spermatozoa are stored prior to ovulation. With certain forms it is known that the male deposits

clumps of sperm in spermatophores on the bottom of the spawning pool, which are subsequently taken up into the cloaca of the female. This condition is inferred in other forms. So far as known to the writer, no case of internal fertilization through direct transference of sperm has been discovered among the Caudata, nor is there any instance of external fertilization such as obtains among the Salientia. The exact method of fertilization in *Dicamptodon ensatus* is unknown. Should it prove to be as outlined above for numerous eastern species and as definitely observed in the case of *A. punctatum* in Michigan (B. G. Smith, 1907, pp. 381–384), namely, by spermatophores subsequently taken up by the female, an avenue of entrance for the spores of the alga would be in association with the spermatophores when taken into the *receptaculum seminis.* Subsequently the spores would have to travel or be carried up the oviduct anterior to the area where the jelly coat of the egg is secreted in order to be included *within* the capsule in which the egg lies. It seems improbable that the alga would make its way into the jelly mass *after* the latter had been extruded, particularly as the alga cells when found in the jelly mass are of a non-motile type. In egg masses of some species of amphibians, however, certain fungi are known to penetrate the jelly and attack dead eggs or larvae while the latter are still in the capsules.

The second question, as to why the algal coating is found in the egg capsule, cannot be answered definitely. The egg masses are deposited in pools of clear water, such as are inhabited by trout, and therefore must contain a fair amount of oxygen. Because of the coldness of the water, development is probably somewhat prolonged. The alga may possibly be of service in oxidizing katabolic products which otherwise might accumulate within the capsule in harmful concentration. In the few egg mases of this species of salamander which have come to my attention there have been practically no eggs which failed to develop. The percentage which develop to the hatching stage seems to be higher than, for example, in the eggs of *Triturus torosus,* where it is known that a considerable number fail to develop far enough to leave the jelly mass.

The embryos prior to hatching attain a length such that they become curled up within the capsules. At hatching they are 15 to 17 millimeters in total length. Unlike the larvae of the Salientia, these young salamanders are active almost at once, and they dart about an aquarium at a relatively high rate of speed. Cope (1889, p. 114) states that he observed larvae in some tributaries of the McCloud

River near Baird, Shasta County. "They swam with great rapidity, darting about and hiding themselves among the fallen leaves that covered the bottom. . . . They are common in the mountain streams of northern California and western Oregon" (Cope, *loc. cit.*).

The only definite information available as to time of hatching is that afforded by the material sent from Costen Lake in 1923 in which some of the larvae hatched one or more days prior to April 28, as evidenced by the empty capsules collected on that date. The last of these would probably have been out by May 1 or shortly thereafter. On May 6, 1923, the writer collected three small larvae of this species in some quiet water on the Olema Creek marshes near Point Reyes Station, Marin County. These were probably hatched about a week earlier. A specimen collected in a roadside pool near Lagunitas, Marin County, on March 9, 1913, is 51 millimeters in total length. Two others taken at Lagunitas, April 21, 1918, measure 61 and 64 millimeters, respectively. These, if of the broods of their respective years, would indicate extremely early dates for egg deposition. On the other hand, they may have been small individuals of the brood of the preceding year, which wintered over in the sizes indicated.

Exact information concerning the rate of development of the larvae is not available; but something of value in this connection may be learned by a consideration of the material which has been collected at various localities in the Coast Ranges of northwestern California during the past fourteen years. The following table lists all the material to which the writer has access at the present time.

LARVAL SPECIMENS OF *Dicamptodon ensatus*

M. V. Z. No.	Locality (in California)	Date of capture	Total length in millimeters
4812	Lagunitas, Marin Co.	Mar. 9, 1913	51
6734	Lagunitas, Marin Co.	Apr. 21, 1918	61
6735	Lagunitas, Marin Co.	Apr. 21, 1918	64
——	Costen Lake, Mendocino Co.	Apr. 28–May 1, 1923	15–17[1]
——	Marsh west of Pt. Reyes Station, Marin Co.	May 6, 1923	18
8568	Costen Lake, Mendocino Co.	June 18, 1922	49
4965	7 mi. w. Cazadero, Sonoma Co.	June 23, 1913	46
4925	Gualala, Sonoma Co.	July 6, 1913	86
4927	Mendocino City, Mendocino Co.	July 13, 1913	77
4928	Mendocino City, Mendocino Co.	July 13, 1913	80
9146	Carlotta, Humboldt Co.	July 27, 1923	82
2342	Fair Oaks, Humboldt Co.	Aug. 24, 1910	207
2343	Fair Oaks, Humboldt Co.	Aug. 24, 1910	228
6342	Muir Cañon, Marin Co.	Sept. 30, 1917	54 to 142[2]

[1] Just hatching. [2] 40 specimens.

The forty larvae collected on September 30, 1917, range from 54 to 142 millimeters in total length. Omitting the longest the others range evenly, without a significant break, from 54 to 119 millimeters. The gradation in size is so even as to suggest that they all came from eggs laid in the spring of that year. If the general run of individuals could increase from 15 to 17 millimeters (the length at hatching) to the various sizes indicated, it seems possible that one individual, particularly fortunate as to food, might increase from 15 to 142 millimeters in one season.

In certain other amphibians it has been found that little growth occurs during the winter season (see, for example, *Rana b. boylii*, p. 255). That this condition obtains in *D. ensatus* is suggested by the following facts. The largest larva in the group just discussed is 142 millimeters long. It was collected on September 30. The larva seen in Costen Lake on June 18 was estimated to be about 150 millimeters long. The only larvae larger than these are the two collected at Fair Oaks, Humboldt County, on August 24, 1910. These measure 208 and 228 millimeters respectively, in total length. It seems likely that these were in their second (or third) summer of growth.

In the series of transformed animals at hand only three of the eleven specimens measure less than 200 millimeters in total length. This seems significant in relation to the probable size of the larvae at transformation. With most species of amphibians, individuals of small or medium size constitute a majority of those seen in the field. While selection of the larger individuals may possibly be practiced by some collectors, it is generally true that specimens are taken, big or small, as they can be obtained. Large frogs often escape by reason of greater wariness or better ability in leaping, and this tends to offset any selective action on the part of a collector. The case with *Dicamptodon ensatus* is different. It is generally considered as a 'rare' species and in the adult form has no particular means of escape. Collectors are therefore likely to bring in every individual which comes to notice. Were it a common thing for the larvae of this species to transform at small size (between 125 and 200 millimeters), more small non-gilled individuals would be expected in our collections. The few small-sized adults which have been collected may represent individuals which, because of changed conditions in the water, transformed earlier than is usually the case. Cope (1889, p. 49) states that the size at loss of branchiae in *tenebrosus* [= *ensatus*] is 5 inches 9 lines (146 millimeters). The number of specimens examined is not given. The same author (p. 506) mentions a larva 250 mm. in length.

The foregoing suggests the following as the probable seasonal history for *Dicamptodon ensatus.* Eggs are laid early in the spring and the embryos hatch out by late April or early May. By autumn the larvae measure from 54 to 119 millimeters, exceptionally 142 millimeters, in total length. Some may metamorphose in the autumn or winter of the year in which they were born, but the majority continue as larvae, growing but little in the ensuing winter. The following summer (possibly two years are required) they reach a length of 200 millimeters or more and then metamorphose. Exceptional individuals come to sexual maturity as larvae. Maximum size of adults is between 280 and 300 millimeters.[4]

One specimen in the axolotl stage (sexually mature larva retaining gills) has come to notice. It was taken in Muir Woods, Marin County, in April, 1897, and was kept alive in the zoological laboratory at Berkeley by Professor H. P. Johnson until July 26, 1897. On that date it was preserved. Gills were still present. Upon being opened, the body cavity was found to contain a large mass of eggs. These eggs, after 26 years in alcohol, measure about 6 millimeters in diameter. The 'axolotl' now measures 247 millimeters in total length.

Food.—The young larvae, when kept in an aquarium, begin feeding upon small aquatic animals such as copepods within a few days after hatching. As growth proceeds, larger items are taken. Cope (1889, p. 114) records that at Baird he took from the stomach of one larva another of the same species, one-third its size. After metamorphosis terrestrial animals are taken as food. An adult individual which the writer once had in captivity fed upon individuals of *Batrachoseps attenuatus* kept in the same terrarium. Another large adult was kept with two *Triturus torosus* for two weeks without molesting them in the least. But later, when a large example of *Aneides lugubris* was placed with the *D. ensatus,* the latter, within 15 minutes, had seized and nearly swallowed the *Aneides.* Other observers have found specimens of the large slug (*Ariolimax*) eaten by *D. ensatus.* One of these salamanders (no. 4841, Mus. Vert. Zool.) collected in a spring 4 miles west of Sausalito, had shells of land snails in its stomach. The stomach of another (no. 2405, Mus. Vert. Zool.) held remains of a land snail and insect fragments. Miss Una Boyle has told the writer that she once came upon a large 'gray' salamander

[4] In late July of 1924, three sizes of larvae were seen in creeks near Carlotta, Humboldt County. The smallest was obviously from eggs of the current season, the second (about 150 millimeters in total length) could scarcely have been less than one year old, while the largest was fully 250 millimeters in length and contained developing ova.

swimming in a creek in the redwoods of Mendocino County with a white-footed mouse (*Peromyscus*) in its mouth.

These fragmentary data indicate that the species is a 'carnivore' with respect to amphibians and land mollusca, and possibly small mammals. In this connection it is interesting to note that more species (and probably also individuals) of salamanders (Plethodontidae and Ambystomidae) occur within the range of *Dicamptodon ensatus* than in any other area on the Pacific slope.

The life-history in relation to the environment.—*Dicamptodon ensatus* is an inhabitant of the northwest humid coast belt. Its range embraces nearly all of the area occupied by the coast redwood and in addition the western portions of Oregon and Washington. It inhabits the territory occupied by the shrew-mole (*Neürotrichus*), Townsend mole (*Scapanus townsendii*), mountain beaver (*Aplodontia*), winter wren (*Nannus hiemalis*), and other species of vertebrates whose prime environmental requirement seems to be moisture in large amount. Its habitat is at all times moist with respect both to atmosphere and soil. The coastal region from Monterey Bay northward to Puget Sound experiences a large amount of rainfall (26.8 inches at Santa Cruz to 78.2 inches at Astoria and 37.0 inches at Seattle); and through the year, particularly in the summer season, there are many days with heavy fog. The mat of leaf mold on the ground in the redwood-Douglas-spruce forest is at all times damp. Further, there is heavy deposition of dew almost every night during the year. In consequence of these features it is possible for a moist-skinned animal the size of *Dicamptodon ensatus* to forage at night and even in the daytime without danger of desiccation. The restriction of the species to the humid area here indicated and the large size to which it attains are probably closely related circumstances. This, so far as the writer knows, is the largest Nearctic species of urodele exclusive of the permanently aquatic *Necturus, Amphiuma,* and *Cryptobranchus.*

In the developmental program a few features of possible adaptive significance may be noted. The firm texture of the egg mass, in conjunction with its large size and its fixation below the surface of the water, together with the probability of a prolonged developmental period, would seem to indicate effective protection for the eggs and embryos prior to hatching, more necessary here than in a short embryonic development, as in the Salientia. The green algal coating in the egg capsule may be of advantage in disposing of waste products of metabolism resulting from development. The active nature of the

larvae and their habit of seeking the bottom of deep pools would remove them from possible enemies at the margin of the water. The cool water in which development occurs probably is responsible for the prolonged larval development. No particular disadvantage would seem to accrue as a result of this feature because the creeks of the 'fog belt' are practically all perennial, and they do not fluctuate greatly in volume of water, between the rainy and dry seasons. Neoteny (cf. Gadow, 1901, pp. 63–64), if it occurs in nature, would simply continue the protection afforded by the aquatic environment.

Batrachoseps attenuatus (Eschscholtz). Slender Salamander

(Pl. 9, figs. 21, 24)

Salamandrina attenuata Eschscholtz (1833, pt. 5, p. 1, pl. 21). Original description, type from vicinity of San Francisco; followed (pp. 1–6, pl. 21) by anatomical account by Rathke.

Batrachoseps attenuata, Baird (1850, p. 288). Monograph.

Batrachoseps attenuatus, Cooper (1868, p. 8). General range.

Batrachoseps nigriventris Cope (1869, p. 98). Type locality, Ft. Tejon, California.

Batrachoseps attenuatus, Strauch (1870, p. 84). Monograph.

Batrachoseps attenuatus, Boulenger (1882*b*, p. 60). Description.

Batrachoseps nigriventris, Boulenger (1882*b*, p. 60).

Batrachoseps attenuatus, Yarrow (1883, pp. 21, 152). Locality records.

Batrachoseps nigriventris, Yarrow (1883, pp. 21, 153), part.

Batrachoseps pacificus, Yarrow (1883, pp. 21, 153), part.

Batrachoseps attenuatus, Cope (1889, pp. 127–128, text fig. 28). General account.

Batrachoseps pacificus, Cope (1889, pp. 129–130), part.

Batrachoseps nigriventris, Cope (1889, p. 129).

Batrachoseps attenuatus, H. H. Wilder (1896, pp. 189–190, 191). Lungless condition.

Batrachoseps attenuatus, Hubbard (1903, pp. 158, 163). Habits at Berkeley.

Batracoseps attenuatus, Whipple (1906*b*, p. 256). Note on anatomy.

Batrachoseps attenuatus, Hilton (1909, pp. 53–54). Locality records.

Batrachoseps attenuatus, Jacob (1910, pp. 280–282, figs. 1–3, pp. 298–300, 329–330). Historical; habits in captivity.

Batrachoseps attenuatus, Burke (1911, pp. 413–414). Eggs and young near Stanford University.

Batrachoseps attenuatus, Camp (1915, pp. 329, 330). Critical; locality records.

Batrachoseps attenuatus, Ruthling (1915, p. 62). In Santa Monica Mountains.

Batrachoseps attenuatus, Fowler and Dunn (1917, p. 26). Critical; locality records.

Batrachoseps attenuatus, Grinnell and Camp (1917, pp. 136–138, fig. 3). Range.

Batrachoseps attenuatus, Stejneger and Barbour (1917, p. 13; 1923, p. 8). Range.

Batrachoseps attenuatus, Stephens (1921, p. 59). In San Diego County.

Batrachoseps attenuatus, Snyder (1923, pp. 86–88, 2 figs.). Eggs and development at Palo Alto.

Batrachoseps attenuatus, Grinnell and Storer (1924, p. 654). At Snelling, Merced County; eggs.

Diagnosis.—Size small, total length up to 130 millimeters (5⅛ inches); body worm-like, greatest diameter less than 10 millimeters; limbs very small, digits 4 on each foot; costal folds 19 (rarely 18 or 20); naso-labial groove present; general coloration everywhere black, usually with broad, straight margined reddish brown stripe along dorsal surface.

Comparisons.—Distinguished from all other California salamanders (except other species of *Batrachoseps*) by slender worm-like form of body, reduced size of limbs, presence of only 4 digits on hind foot and costal folds numbering more than 15 between axilla and groin; from *Batrachoseps major* by 19 instead of 18 costal folds, by presence of dark line along side of body, and by dark instead of yellowish undersurface; from *B. pacificus* by 19 instead of 16 (15 or 17) costal folds, smaller size of orbit, less broad head and blackish instead of brownish coloration of undersurface; from *B. catalinae* by larger size, better development of inner digit on each foot, and darker coloration of ventral surface.

Description.—Body slender, worm-like, head not wider than body, limbs reduced, tail exceeding body in length; head oval or bluntly oval in outline from above; muzzle short, thick in profile; external nares subterminal, below canthus rostralis, directed dorsally; naso-labial groove exceedingly minute; canthus rostralis slightly longer than orbit; eyes large, protruding from top of head, interorbital space about two-thirds length of orbit, sometimes with shallow furrows; head not wider than body, nearly as deep (thick) as wide; neck region scarcely constricted; lower jaw acutely oval in outline; gular fold slight; two or three transverse grooves on neck, connected with orbit by lengthwise furrow on side of neck; limbs all very short and slender; length of limbs not more than greatest diameter of body; free portion of upper arm slightly longer than forearm; palm small; digits 4, short, blunt ended, in order of decreasing length 3, 2, 4, 1; body slender, cylindric, scarcely swollen at midlength; mid-dorsal groove distinct; costal folds 19, well indicated; hind limb scarcely larger than fore limb; femur about as long as tibia; toes 4 in number, third longest, second and fourth about equal, first much shorter; tail (when unbroken) exceeding body in length, slightly wider than high at base, tapering (if not injured and reproduced) evenly to end, marked laterally with numerous transverse grooves.

Tongue thin, rounded, its diameter about half width of mouth at angle of jaws, pediceled and freely protrusible; maxillary teeth relatively large, scattered; internal nares well up in anterior part of mouth and close to margin of jaw; vomerine teeth in two separate but convergent patches posterior to internal nares; parasphenoid teeth separated from vomerine teeth by short interval, in one broad patch widest posteriorly. Surfaces everywhere smooth.

General coloration in life, black; mid-dorsal surface from neck region to near end of tail, usually with broad stripe of dark reddish brown; lateral and ventral surfaces with innumerable minute points of white.

MEASUREMENTS OF ADULT SPECIMENS OF *Batrachoseps attenuatus* FROM CENTRAL CALIFORNIA

M. V. Z. No.	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4955[1]	June 12, 1913	82	45	6.7	4.2	2.1	1.4	5.2	1.5	22.3	5.0	2.0
4954[1]	June 12, 1913	93	49	6.5	4.1	1.9	1.3	5.2	1.4	26.7	5.3	1.8
4952[1]	June 12, 1913	93	50	7.6	4.2	2.3	1.4	5.4	1.4	28.2	5.4	1.4
9159[2]	July 26, 1923	98	54	7.1	4.3	2.2	1.0	5.4	1.8	28.8	5.7	1.6
2385[3]	Feb. 22, 1910	112	65	8.0	5.1	2.2	1.3	5.4	1.8	29.0	5.2	1.9
8249[3]	Mar. 14, 1905	115	70	7.7	....	2.0	1.4	5.7	1.8	30.8	5.8	1.5
8250[4]	Mar. 14, 1905	116	65	9.0	6.4	2.3	1.5	7.0	1.6	33.7	7.0	2.2
8247[4]	Mar. 14, 1905	118	66	9.5	6.0	2.3	1.7	5.6	1.8	33.5	5.7	1.7
9160[2]	July 26, 1923	120	69	7.8	4.1	2.0	1.2	5.2	1.6	34.0	5.6	1.8
8248[4]	Mar. 14, 1905	130	78	8.0	7.1	2.2	1.4	5.2	2.2	33.5	5.4	2.6

[1] Freestone, Sonoma Co.
[2] Carlotta, Humboldt Co.
[3] Near Berkeley, in Contra Costa Co.
[4] Berkeley, Alameda Co.

History.—*Batrachoseps attenuatus* was discovered by Eschscholtz during his second visit to California in 1824 and a specimen collected by him was described in his Zoologischer Atlas. Eschscholtz' meager description was supplemented by a six-page account of the anatomy of the species by Rathke. Cope in 1869 described material from Fort Tejon as *Batrachoseps nigriventris.*

Range.—This species has been found at the north in southwestern Oregon (Stejneger and Barbour, 1917, p. 13), more definitely, Gold Beach and Harbor, Curry County (specimens in Calif. Acad. Sci.); in California it is present in the coastal region from Crescent City, Del Norte County (Calif. Acad. Sci.) south to San Diego (Calif. Acad. Sci.), extending inland to near Napa, Napa County, and to "hills back of Livermore," Alameda County (Mus. Vert. Zool.). Specimens from Angel Island in San Francisco Bay are in the collection of the California Academy of Sciences. Dunn (1918, p. 439) has recorded this species from Sacramento; but the record needs confirmation. In the Sierra Nevada it has been taken from Eldorado County southeast to 3 miles south of Nelson, Tulare County (Grinnell

leaves. On December 13 after the population had been established aboveground for some time, the hiding place was examined at 6:15 P.M. after full darkness. There were no salamanders under the box, but, by aid of the flash lamp, one was seen out on a path where none could be found during the daytime. On December 28 more than 20 *Batrachoseps attenuatus* besides four large *Ensatina eschscholtzii* were found under this particular box.

When the hiding place of *Batrachoseps* is uncovered during the daytime some of the animals remain quietly in place. Others make off by creeping along as fast as is possible with their small legs and feet; still others suddenly curl the body into an irregular loop and then suddenly straighten out, sometimes continuing this as a series of violent contortive movements, curling first to one side and then to the other. The result is to carry the animal in irregular course this way and that. An attempt to pick up one of the salamanders often stimulates the animal to begin these peculiar movements. None of our other salamanders has been seen to do this; it is probably correlated with the relatively slight development of the limbs in *Batrachoseps*. The successive movements are executed in quick succession and would seem to be of service in evading natural enemies. The ordinary slow walking motion would be of no avail to *Batrachoseps* in an emergency.

A second feature of possible service in case of attack by an enemy is the autotomy of the tail. Specimens of *Batrachoseps* when seized by the tail can break it off with reasonable facility by giving it a few violent sidewise twists. Whether this feature is of actual service to the salamander is unknown. In the case of captive individuals attacked by other species of salamanders (Storer, MS) or by snakes (Hubbard, 1903), enemy and prey were in close confinement so that the experiments are not conclusive with respect to the possible service of the tail under natural conditions.

In the winter of 1921 the writer had several specimens of *Batrachoseps attenuatus* confined in a terrarium with a specimen of *Ambystoma californiense*, three adult *Triturus torosus*, and an adult and young of *Ensatina eschscholtzii*. The *Batrachoseps* were seen to be decreasing in numbers and one day the *Ambystoma* was discovered with the tail of a *Batrachoseps* protruding from its mouth. Later the tails of two more were found, evidently severed when in the mouth of the larger salamander. *Aneides lugubris* has been known to feed on *Batrachoseps* on at least one occasion. Hubbard (1903, p. 163) records *Batrachoseps* as having been fed upon by two snakes,

and Camp, 1917, p. 137). In southern California it has been obtained at Fort Tejon, Kern County (Cope, 1869, p. 98), in the Santa Monica Mountains, Los Angeles County (Ruthling, 1915, p. 62), eastward to mountains north of Claremont (Grinnell and Camp, *loc. cit.*). This species has been recorded on San Pedro Martir Mountain, Lower California (Van Denburgh, 1895*a*, p. 560). There is also a record for a Batrachoseps at La Paz but this needs confirmation, as no specimens have been obtained there in the last forty-four years despite the number of collectors who have visited the region.

Life-history.—This salamander is abundant in most parts of its range during the wet season, but as soon as the ground becomes dry it retires beneath the surface and is seen no more until the next rainy period. During the rainy season any log, stone, or board on the ground under or adjacent to the shade of trees in the foothill country will usually have one or more of these animals under it.

Wherever found *Batrachoseps attenuatus* is strictly terrestrial although captive individuals have occasionally been observed to climb the sides of glass-walled terraria in which they were confined. In a state of nature the animals live under objects resting on the surface of the ground where moisture is conserved, in the cavities of rotted stumps or logs, and in leaf mold.

On the University of California campus at Berkeley this salamander is normally abundant. In 1921 watch was kept of suitable retreats for the species adjacent to the Museum of Vertebrate Zoology, and fully 50 of the animals were present under boxes and boards within 20 feet of the building. They disappeared entirely in early May, but with the first rains of the autumn (November) they reappeared in customary numbers. Upon visiting a certain box under a grove of Pittosporum trees 15 or more were usually to be found during the daytime. In late February all of the *Batrachoseps* occurring there were collected; within ten days a dozen or more additional animals were found. On succesive days the population was different in numbers and distribution suggesting that these salamanders do not have so fixed a 'homing' response as do toads. On the night of March 7 I visited the box at 11 P.M. and found only two salamanders present. The ground and leafy débris adjacent were examined carefully with the aid of an electric flash lamp but none of the animals could be seen. Next morning the space under the box was found to harbor the usual number of salamanders; in addition to these, two individuals were found on the surface of the ground away from the box, but under some

Thamnophis elegans (ssp.?) and *Diadophis amabilis*. She says: "At least five tests were made with the Batrachoseps in connection with these two snakes. The taste is perhaps not quite to the snake's liking, for in some cases there was a slight gaping after eating, but in no instance was there the least hesitation in attack. Only once did regurgitation occur and this once it may have been due to over-eating, for the snake had devoured three or four Batrachoseps in quick succession."

Batrachoseps attenuatus breeds during the winter rainy period in central California. Eggs of this species were first discovered and described by Burke (1911, pp. 413, 414) from Stanford University, January, 1906, and January 5, 1907. On January 8, 1915, eggs, probably of this species, were found at Snelling, Merced County (Grinnell and Storer, 1924, p. 654). Dr. V. E. Emmel obtained a set advanced in development at Berkeley on March 7, 1920, and Snyder (1923, pp. 86–88) obtained eggs at Palo Alto, Santa Clara County, March 14, 1922.

Burke (1911, p. 414) says:

> The first eggs obtained were discovered by T. Kimura during January, 1906. They were found partly buried in depressions under rocks on a moist hill side. On January 5, 1907, the author found some eggs under a log in a moist ravine well up in the hills near Stanford University. The eggs were deposited in small pockets in the ground; 21 were in one group and 10 in another group about 2 feet distant, while 4 were scattered between, suggesting that all were deposited by a single female. These eggs were round or slightly oval and about 6 mm. in diameter. Development was well advanced. The first individual to issue from the egg appeared on January 28, and was 17 mm. in length and of a dull black color. By May 22 it had doubled in length and was 35 mm. long. The majority of the eggs, when found, were covered with a fungus and failed to develop. This suggests that they may have been under abnormal conditions. It seems very likely that the majority of the eggs of this species are deposited just beneath the surface of the ground, as is the case with earthworm eggs, and so escape detection. Diligent search at the proper season should settle this question.

The material at Snelling consisted of about 15 eggs. The lot obtained by Dr. Emmel (Storer, MS) was found under a plank in a moist springy place near a brush pile in Strawberry Cañon. There were 53 eggs in all. The limb buds of all the legs of the embryos were about 1.5 millimeters long. The gills were in evidence but there was no trace of a tail fin. On March 15, two embryos removed from their capsules measured 13 to 14 millimeters in total length. The gills were almost entirely resorbed by the time of hatching, which for some of the eggs occurred on March 20.

Snyder (1923, pp. 86–88, 2 figs.) has described eggs of this species found at Palo Alto, Santa Clara County, March 14, 1922. The eggs were with the parent in a small pocket beneath the surface of the soil in a garden. The eggs were

very firm, gelatinous globules, securely attached, one to another, much like loosely strung beads.

Each egg measured 6.3 millimeters in diameter. The capsule was almost perfectly transparent and of a pale amber color. When placed in water and viewed by transmitted light, the embryo appeared to be enclosed by two distinct capsules, one within the other. The outer, when dissected away, was dense or rigid enough to maintain its globular form. Its substance was amber-colored, whilst the capsule within was colorless. Extending from each pole of the outer capsule was a filament by which it was attached to the adjoining egg. The filament did not appear to be hollow. The inner capsule could not be made to revolve within the outer one, although the two readily separated.

The embryo could be observed through the second capsule as clearly as if it had been embedded in optical glass. It was curled about a large straw-colored mass of yolk, the tail passing to one side of the head in one case, a little below and posterior to it in another. At this time the legs were well developed and large trilobed gills were present. It will be recalled that *Batrachoseps* is terrestrial, and is never seen in the water. It could not be determined whether the gills were functioning as organs of respiration.

The second enclosing capsule was dissected away, but unlike the first one, it fell into a shapeless mass. It was removed with difficulty, being very elusive, easily evading the edge of the scalpel. It was now seen that the embryo was within still another capsule, the substance of which was very viscid and adhered closely to an inner membrane. When the latter was laid bare it quickly shrunk as if a contained fluid had passed out, compressing the embryo from all sides into the least possible space. When the membrane was ruptured the body of the embryo straightened out like a released spring.

At the stage here described the embryo measured about 10 millimeters in length. When it grew to about 13 millimeters, and the yolk mass was considerably reduced, the gills were much shortened. Later, when the embryo was about 16 millimeters long and the remnant of the yolk, enclosed within the body, was just visible through a long abdominal slit, the gills had nearly disappeared. Shortly after this, April 3, one salamander hatched. It measured 16.5 millimeters. No gills were visible.

The writer has not observed the slender salamander burrowing in the ground, certainly not after the manner of the earthworm, as alluded to by Dr. Burke.

Two embryos dissected out of the Berkeley material, several (5–10) days before other eggs in the lot began hatching, are provided with very slender gills; on one of the animals the gills consist of three slender filaments on each side. The yolk mass is still in evidence. These embryos measure nearly 14 millimeters in total length. Three young preserved 5 to 10 days after hatching (which occurred March 20, 1920) likewise measure 14 millimeters. A young animal collected in another part of Berkeley on May 2, 1920, is but 16 millimeters long

and hence had probably hatched out a few days earlier. One collected in Bailey Cañon, 3000 feet, near Sierra Madre, Los Angeles County, on April 4, 1908, is 21 millimeters in length. Three others obtained in the San Gabriel Mountains nearby, at 3000 feet, on June 16, 1909, are 25, 25, and 31 millimeters, respectively, in length. The breeding season of *attenuatus* in the central and southern parts of the State would appear to be about the same.

One recently hatched young *Batrachoseps*, from the eggs collected at Berkeley, measured as follows: total length 19 mm.; length of tail 6 mm.; width of head 2 mm.; center of foreleg to center of hind leg 7 mm. The general coloration was black, with a slight brownish tinge; on the back were four parallel lines of spots silvery white and reddish gold in color; the ventral surface of the body was marked generally with scattered patches of silvery white. The costal folds were 17 in number, the external nares relatively large and directed anteriorly; the naso-labial groove, if present, could not be distinguished.

One adult collected at Berkeley had two small weevils and several small beetle larvae in its stomach. Another, seen under a board, had nearly devoured an earthworm. Captive specimens of *Batrachoseps* can be fed successfully with fruit flies (*Drosophila*).

Eisen (1897; 1900*a*, *b*) and Emmel (1920) have used this species in cytological and haematological studies. Its small size, and the possibility of providing a steady source of food in the form of the fruit flies bred successfully for studies in genetics, would suggest *Batrachoseps* as a suitable species to keep on hand, "domesticated," in cytological laboratories. This salamander is peculiar in having non-nucleated erythrocytes (see Eisen, *loc. cit.*; Giglio-Tos, 1899).

A large series of specimens of *Batrachoseps* collected near Napa, Napa County, December 16, 1912, is available for the study of growth. This series, taken at one place and time, ought to indicate any age-grouping which might occur in the population. The 87 individuals, in condition for satisfactory measurement, were found to group as follows:

Total length in millimeters:	33–40	41–50	51–60	61–70	71–80	81–90	91–98
Number of specimens	2	1	6	17	31	22	8

Burke's specimen grew from a length of 16 millimeters on January 28 to 35 millimeters by May 22. The latter date marks the approximate time of disappearance of *Batrachoseps* from the ground surface. If the animals actually aestivate during the dry season then the individuals under 50 millimeters in the tabulation just given would

be 'yearlings' and the group centering around 75 millimeters (60–90 mm.) would be two-year-olds. If, on the other hand, growth is continuous during the summer season then the animals in the table must be considered as all representing one year group, with a mean length of 70.5 millimeters being attained the first year. The matter cannot be decided. There are individuals of *Batrachoseps attenuatus*, however (see table of measurements) considerably over 100 millimeters in length and these, without doubt, are two years, or more, of age. It would seem that *Batrachoseps* arrives at sexual maturity when about two years of age, a condition parallel to that in the Hylidae, but different from that in other amphibians, most of which seem to require three years of growth before breeding.

The life-history in relation to the environment.—*Batrachoseps attenuatus* (and its generic relatives) is the smallest amphibian and the smallest land vertebrate in California. In the elongation of the body, increase in number of costal (vertebral) segments, reduction in size of limbs and feet, and elongation of tail we see in this salamander definite specialization toward subterranean life. In the Plethodont fauna of California the aboveground niche is filled by *Aneides*, the surface burrows of rodents are used by *Ensatina*, and *Batrachoseps* uses openings in the ground smaller than those available to either of the other two. There is no evidence that *Batrachoseps* actually burrows in the ground as Burke (1911) surmised, but I do believe that these salamanders are able to and do use the excavations made by earthworms and insects of various kinds. During the winter rainy period any sort of daytime cover is utilized as a temporary refuge; with the arrival of the dry season a definite movement into the ground removes the animals from danger of desiccation. They disappear regularly as the surface of the earth dries out and reappear immediately upon the advent of soaking rains in the autumn. Egg laying occurs in the latter part of the winter rainy period. Were the salamanders to mature their sex products during the summer dry period while in underground shelters, intermingling of the sexes for the purpose of mating would be less likely to occur; if they appeared at the surface of the ground in that time of year, death by desiccation would be much more likely for both themselves and their eggs. With the breeding period in the rainy season, danger of desiccation is avoided and food is available, both for the adults and later for the young, permitting the latter to make a considerable increase in size before the summer season arrives.

Batrachoseps catalinae Dunn. Catalina Island Salamander

Batrachoseps attenuatus, Van Denburgh (1905, pp. 3, 16). On Santa Catalina Island, California.
Batrachoseps attenuatus, Van Denburgh and Slevin (1914, pp. 132, 137).
Batrachoseps catalinae Dunn (1922*b*, pp. 62–63). Original description, type from Santa Catalina Island, California.

Diagnosis.—Size small, total length up to 121 millimeters (4¾ inches); body worm-like; limbs small, digits reduced to 4 on each foot, innermost rudimentary; costal grooves 19 to 21 [costal folds 18 to 20?]; coloration dull brown above, paler beneath; vomerine teeth in irregular patch.

Comparisons.—Distinguished from all other California salamanders except species of *Batrachoseps* by slender worm-like body, reduced limbs, and presence of more than 15 costal folds; from *Batrachoseps attenuatus* by smaller size, rudimentary inner digit, and paler coloration especially on ventral surface; from *B. major* by smaller size, and rudimentary inner digit on all feet; from *B. pacificus* of the northern Channel Islands by 18 to 20 instead of 16 costal folds. [Diagnosis and comparisons based on data in original description; no specimens at hand.—T. I. S.]

Range.—This species is restricted to Santa Catalina Island, off the coast of Los Angeles County, California.

Remarks.—Van Denburgh (1905, p. 16), while placing salamanders from Santa Catalina Island, California, under the name of the mainland species *Batrachoseps attenuatus*, gives the coloration of one individual as "uniform slaty brown above, paler below" and states that three others differ "from this one only in the slightly paler coloration." Van Denburgh and Slevin (1914, p. 137) say that "the salamanders of Catalina seem not to differ from those of the mainland."

As Dunn (1922*b*, p. 63) points out, his *catalinae* is not similar in coloration to *attenuatus*; the latter has a light dorsal band (stripe), whereas *major*, *leucopus* [of Los Coronados Islands], and *catalinae* are the reverse of this, with the lighter color area on the ventral surface.

In the absence of material I am unable to pass definitely upon the status of Dunn's form, but from the description he gives I am inclined to believe that the Catalina salamander constitutes a valid species, though distinguished but slightly from the mainland stock. Parallel cases of slight differentiation are afforded among other classes of vertebrates such as *Urocyon catalinae*, *Reithrodontomys m. catalinae*, *Peromyscus m. catalinae*, *Citellus b. nesioticus* among mammals, and

Lophortyx c. catalinae, and *Thryomanes b. catalinae* among birds. The reptiles of the island and the one other amphibian (*Hyla regilla*), however, are not reported to exhibit any differences from their respective mainland stocks (Van Denburgh and Slevin, 1914, pp. 137–139).

Batrachoseps major Camp. Garden Salamander

[?]*Batrachoseps attenuatus*, Cope (1883, p. 28). At Pasadena, California.

Batrachoseps major Camp (1915, pp. 327–330). Original description, type from Sierra Madre, 1000 feet, Los Angeles County, California.

Batrachoseps major, Grinnell and Camp (1917, p. 136, fig. 3). Range.

Batrachoseps major, Fowler and Dunn (1917, p. 26).

Batrachoseps major, Stejneger and Barbour (1917, p. 14; 1923, p. 9). Range.

Diagnosis.—Size small, total length up to 162 millimeters (6⅜ inches); body worm-like, less than 10 millimeters in diameter; limbs very small, digits 4, 4; costal folds 18 (less often 17 or 19); naso-labial groove present; coloration (in alcohol) above, light neutral gray; lower surface, upper lip, and plantar surfaces of feet, cream buff.

Comparisons.—Distinguished from California salamanders other than species of *Batrachoseps* by worm-like form of body, reduced limbs, presence of only 4 digits on hind limb, and 17 or more costal folds; from *Batrachoseps attenuatus* by 18 instead of 19 costal folds, yellow instead of dusky coloration of undersurface, absence of dark line on side of body, and by large adult size, proportionately wider head, longer limbs, and shorter tail; from *B. pacificus* of the Channel Islands by 18 instead of 16 costal folds, and by relatively narower head, shorter limbs, longer tail, and larger size; from *B. catalinae* of Santa Catalina Island by better development of innermost digit on each foot and by larger size.

Description.—Body slender, limbs reduced, tail very large and long; head roughly pentagonal and muzzle truncate oval in outline from above; head depressed, greatest width about half thickness; muzzle short, descending in profile, rounded at end and overhanging lower jaw; external nares nearly terminal, opening antero-dorsally, separated by more than width of interorbital space; naso-labial groove minute, on raised ridge; canthus rostralis indistinct, shorter than length of orbit; orbit large; inter- and post-orbital areas flattened, interorbital space less than length of orbit; lower jaw broad, pointedly oval at tip; angle of jaw under posterior margin of orbit; gular fold indistinct; neck constriction slight; upper arm and forearm about equal in length; digits small, blunt ended, third longest, second and fourth equal, innermost (first) reduced; body very slightly swollen at midlength; costal grooves shallow, not extended to dorsal or ventral surface; costal folds 18 (17 or 19); hind limb scarcely stouter than fore limb; femur longer than tibia; foot small; toes 4, blunt, in order of decreasing length 3, 2, 4, 1, latter very short; tail only slightly smaller in diameter than body, circular in section, stout throughout its length, conical at tip, with many transverse furrows on side.

Tongue thin, squarish behind, rounded anteriorly, filling about two-thirds of width of mouth; internal nares and teeth as in *Batrachoseps attenuatus.*

Color (in alcohol) above, light neutral gray; sides, lower surface, upper lip, and plantar surfaces of feet, cream buff; ventral surface of tail and of body between limbs slightly darker (Camp, 1915, p. 329).

MEASUREMENTS OF ADULT SPECIMENS OF *Batrachoseps major* FROM LOS ANGELES AND RIVERSIDE COUNTIES, CALIFORNIA

M.V.Z. No.	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4570	Sierra Madre	Mar. 26, 1909	101	56	9 2	5 4	2 7	1 2	7 0	1.8	28	7.5	2 8
4562	Sierra Madre	Mar. 29, 1909	118	67	10 0	5 4	3 0	1 3	7 3	2 1	32	8 2	3 0
4576	Pasadena	Mar. 31, 1911	123	72	10 2	6 0	3.0	1 4	7 4	2 5	34	8 3	3.0
6736	Riverside	Apr. 15, 1918	125	73	8 6	5 0	2 9	1 2	6 8	2 2	34	7 4	2 2
611[1]	Sierra Madre	Mar. 14, 1909	134 4	79.5	11 3	6 2	3 0	1 4	7.0	..	35	8 4	2.1
4566	Sierra Madre	May 2, 1908	138	81	10 6	5 5	3 4	1 6	8 2	2 7	35	7.7	3 0
4585	Pasadena	Dec. 21, 1910	155	94		6 1	2 5	1 6	9 1	2 8	36	8 7	2.8
956	Pasadena	Apr. 27, 1906	62[2]	....	12 0	6 8	3 3	2 1	8 1	3 0	38	9 1	3 1

[1] Type specimen.
[2] Head-and-body only.

Range.—This distinct species was first described from specimens taken at Sierra Madre and Pasadena, Los Angeles County (Camp, 1915, pp. 327–330). One example was collected at Riverside, Riverside County, about April 15, 1918 (no. 6736, Mus. Vert. Zool.) and two were taken in Orange County, exact locality unknown, in the spring of 1915 (nos. 9139–40, Mus. Vert. Zool.). The Pasadena specimens were taken beneath boards in a yard and in a cellar. At Sierra Madre the animals have been found under a broken cement slab, beneath wet lumber, and in post holes; in August, two were taken several feet beneath the surface of the ground in loose gravel in a ravine bottom (Camp, *loc. cit.*).

Life-history.—Practically nothing is known of the life-history of this species. Camp (*loc. cit.*) states that the localities of capture "lie in the upper edge of the Lower Sonoran life-zone (mesa oak association) and below the range of *Batrachoseps attenuatus.* The latter species appears to inhabit the Upper Sonoran zone. . . . Both species are entirely terrestrial and both appear to aestivate during the drier months, being then seldom found above ground."

Batrachoseps pacificus (Cope). Channel Islands Salamander

Hemidactylium pacificum Cope (1865, pp. 195–196). Original description, type from "Santa Barbara" [=some one of the Channel Islands: see Van Denburgh, 1905, pp. 6–7].

Hemidactylium pacificum, Strauch (1870, p. 76). Monograph.

Batrachoseps pacificus, Yarrow (1883, pp. 21, 152), part.

Batrachoseps pacificus, Cope (1889, pp. 129–130), part. General account.

Batrachoseps pacificus, Van Denburgh (1905, pp. 5–8). Critical; redescription; on Santa Rosa and San Miguel islands.

Batrachoseps pacificus, Van Denburgh and Slevin (1914, pp. 132, 134, 135). Range, coloration, habitat.

Batrachoseps pacificus, Camp (1915, pp. 328–330). Comparisons.

Batrachoseps pacificus, Grinnell and Camp (1917, p. 136, fig. 3). Range.

Batrachoseps pacificus, Stejneger and Barbour (1917, p. 13; 1923, p. 9). Range.

Batrachoseps pacificus, Dunn (1918, p. 458). On Santa Cruz Island.

Diagnosis.—Size small among California salamanders, total length not over 115 millimeters (4½ inches); body slender and elongate; limbs reduced; digits 4, 4; costal folds 16 (rarely 15 or 17); body coloration yellowish brown above, white or dull yellow below.

Comparisons.—Distinguished from other California salamanders (except species of *Batrachoseps*) by slender form of body, reduced size of limbs, and presence of only 4 digits on each hind foot; distinguished from all species of *Batrachoseps* by larger size of eyes, by greater width of head (greater than that of body), and by smaller number of costal folds, 16 (15 or 17) instead of 17 or more.

Description.—Body slender, worm-like, head moderate, limbs small; outline of head from above parallel-sided behind orbits, bluntly oval anteriorly; head thin in profile, muzzle descending anteriorly, tip rounded; lower jaw overhung by muzzle; external nares opening anteriorly; naso-labial groove exceedingly small; canthus rostralis distinct, shorter than orbit; orbit large; interorbital width less than or nearly equaling length of orbit; interorbital and postorbital portion of head flat; three transverse folds on dorsal and lateral surfaces of neck; outline of lower jaw oval; chin flat; gular fold distinct, extending up on lateral surface of neck where joined by sinuous groove running posteriorly from orbit; limbs stouter than in mainland species of *Batrachoseps;* exposed portion of upper arm and forearm equal in length; digits 4, short, blunt, third longest, second and fourth about equal, innermost (first) rudimentary; body practically straight-sided, slightly depressed; costal grooves very distinct; costal folds 16 (15 or 17); hind limb like fore limb, very slightly stouter; inner toe rudimentary; tail at base of same size as body, tapered distally, lateral surface with vertical grooves.

Tongue and teeth as in *Batrachoseps attenuatus.*

General coloration (in alcohol) cinnamon to mummy brown above, paler on head and limbs, often fawn-colored on tail; upper lip and all lower surfaces white or dull yellow; young specimens much darker

than adults; lower surface often minutely dotted with brown. [Description based on four small individuals from San Miguel Island, compared with redescription of species by Van Denburgh, 1905, p. 8.]

Remarks on coloration.—Van Denburgh and Slevin (1914, p. 134) say that one of two specimens collected on San Miguel Island had a reddish dorsal band similar to that seen in some specimens of *B. attenuatus*. The other showed the uniform yellowish brown coloration characteristic of all other known specimens of *B. pacificus*.

MEASUREMENTS OF SPECIMENS OF *Batrachoseps pacificus* FROM SAN MIGUEL ISLAND OFF COAST OF SOUTHERN CALIFORNIA

(Adapted from Van Denburgh, 1905, p. 8.)

Total length	Length of tail*	Snout to gular fold	Greatest width of head	Fore leg	"Between limbs" (axilla to groin?)	Hind leg
45	20	6	3.5	5	15	5.5
67	31	7.5	5	7	22	7.5
113	64	10	7	9	31	9.5
108	56	10	6.5	9	36	9.5
115	63	10	7	8.5	33	8.5
115	59	10.5	8	9	38	10

* Apparently measured from anterior border of anal opening and not posterior border as elsewhere in present paper.

History.—Cope described this salamander in 1865 on the basis of a specimen listed as from Santa Barbara, but which in all probability was secured on one of the islands where the species is now known to occur (see Van Denburgh, 1905, pp. 5–6).

Range.—This species is restricted to Santa Rosa, San Miguel, and Santa Cruz islands in the channel group off Santa Barbara County (Van Denburgh, 1905, pp. 5–6; Van Denburgh and Slevin, 1914, pp. 134, 135). Cope's ascription of this species to San Francisco was, as pointed out by Van Denburgh, undoubtedly due to misidentification of specimens of *attenuatus*.

Life-history.—This species is evidently similar in habits to its mainland relatives. On San Miguel Island it has been found on the ground under a fallen post, and on Santa Cruz Island five were taken under old bark and rotten logs (Van Denburgh and Slevin, *loc. cit.*).

This island *Batrachoseps* is said by Van Denburgh to bear a resemblance to species of *Plethodon*, and in one instance this resemblance is carried farther by the presence of five toes on the hind foot

of a specimen. It may be that *pacificus*, which has the lowest number of costal folds of any member of the genus, and which has also relatively large eyes and wider head and body, is nearest the ancestral stock from which the "slender salamanders" have descended. Isolation upon the Channel Islands, in the absence of competition with other Plethodont species, may have permitted survival in a form less specialized than that required of the mainland stock.

Plethodon elongatus Van Denburgh. Del Norte Salamander

Plethodon elongatus Van Denburgh (1916, pp. 216–218). Original description, type from Requa, Del Norte County, California.
Plethodon elongatus, Grinnell and Camp (1917, p. 134, fig. 2).
Plethodon elongatus, Stejneger and Barbour (1917, p. 15; 1923, p. 10).

Diagnosis.—Size small among California salamanders, total length up to 117 millimeters (4⅝ inches); naso-labial groove present; costal grooves 16 [costal folds 15?]; general form slender; coloration blackish brown, with dorsal stripe of light brown, black edged; ventral surface sprinkled with small dots of white.

Comparisons.—Distinguished from other California salamanders by presence of 16 costal grooves [= 15 folds?], in combination with well developed limbs and presence of light stripe along back; from *Batrachoseps* by better development of limbs and smaller number of costal folds; from *Aneides* and *Ensatina* by larger number of costal folds.

Description (adapted from original description by Van Denburgh, 1916, pp. 216–218).—Snout rounded in outline from above and in profile; head somewhat depressed, width about that of widest part of body; external nares small, internarial space about equal to distance from naris to pupil; naso-labial groove descending nearly to margin of lip; eyes moderate; interorbital space about 1½ times length of orbital slit [not length of orbit as elsewhere in this paper—T. I. S.]; margin of lip bent downward from end of muzzle to below eye; neck a little narrower than body; gular fold "continued up on side of neck and then forward as groove to orbit"; limbs a little stouter than in *P. intermedius* of Oregon; digits 4, rather short, tips rounded, each with small terminal pad, in order of decreasing length, 3, 2, 4, 1, not webbed; adpressed limbs separated by about 6 costal folds; middorsal groove present on back; costal grooves 16 [folds 15?]; second toe shorter than fifth, third and fourth nearly equal; tail cylindroconic, posterior half compressed laterally, with strong vertical grooves nearly to tip.

Tongue large, ovate, not emarginate, attached along median line but free laterally and for a short distance posteriorly; internal nares small; vomerine teeth in two slightly curved series beginning just behind internal nares, converging obliquely backward, separated medially by space greater than diameter of internal naris; parasphenoid teeth in one patch throughout, separated from vomerine teeth by interval equal to distance from [internal?] nostril to edge of lip.

General color above and below, blackish brown; broad dorsal band from snout to base of tail lighter brown, edged with black; lower surface sprinkled with small whitish dots, larger on chin, gular region and sides.

Measurements (of type, from Van Denburgh, *loc. cit.*).—Total length 117 millimeters; tail (from anterior border of anus), 58; snout to gular fold 11; greatest width of head 7.5; snout to orbit 3; foreleg 9; axilla to groin 30; hind leg 10.5; hind foot 5.

Range.—*Plethodon elongatus* is known from four specimens collected at Requa, Del Norte County, May 22 to 26, 1911.

Life-history.—Van Denburgh (*loc. cit.*) mentions a young individual 42 millimeters in length, collected as above. This compares in size with the length attained by other west coast Plethodonts at about one year of age and suggests a summer breeding period for *elongatus.* This specimen (in alcohol) had the dorsal light stripe bright pink, clouded on the head and mid-dorsal line with dark brown.

Ensatina croceater (Cope). Yellow-spotted Salamander

Plethodon croceater Cope (1867, pp. 210–211). Original description, type from Fort Tejon, California.
Plethodon croceater, Boulenger (1882*b*, p. 55). General description.
Plethodon croceater, Cope (1889, pp. 150–152). General account.
Plethodon croceater, Van Denburgh (1916, pp. 220–221).
Plethodon croceater, Grinnell and Camp (1917, pp. 132–134, fig. 2). Range.
Plethodon croceater, Stejneger and Barbour (1917, p. 14). General range.
Ensatina croceater, Stejneger and Barbour (1923, p. 12). General range.

Diagnosis.—Size moderate among California salamanders, total length up to 133 millimeters (5¼ inches); naso-labial groove present; costal folds 10; maxillary and mandibular teeth inconspicuous; body coloration dark reddish brown, with scattered rounded spots, of varying size, of yellow.

Comparisons.—Distinguished from other California salamanders except Plethodontidae by presence of naso-labial groove and parasphenoid teeth; from *Batrachoseps* by development of 5 digits on hind foot, 10 instead of 15 or more costal folds, stouter form of body and spotted pattern of coloration; from *Aneides* by less swollen temporal region, smaller maxillary teeth, 10 instead of 12 costal folds, and presence of spots more than 1.0 mm. in diameter in coloration; from *Hydromantes* by 10 instead of 12 costal folds, less flattened head, smaller maxillary teeth, unwebbed digits and yellow instead of gray markings; from *Ensatina eschscholtzii* by spotted pattern of coloration.

Description.—Form stout among California Plethodontidae, limbs well developed, tail moderate; head truncate oval in outline from above; muzzle thick in profile, rounded at end, scarcely overhanging lower jaw; external nares terminal, opening laterally; sides of muzzle slanting, no distinct canthus rostralis; orbit large, nearly equaling

ante-orbital region in length; upper eyelid broad and thick; interorbital space flat, its width three-fourths or more of length of orbit; conspicuous furrow running backward from posterior margin of orbit on side of head; angle of jaw at or behind posterior margin of orbit; lower jaw oval to nearly semicircular in outline; chin region slightly convex; gular fold very conspicuous, continuing up side of neck, and nearer insertion of fore limb than orbit; fore limb moderate; exposed portion of upper arm shorter than forearm; palm short; two metacarpal tubercles, inner slightly larger; digits short, depressed, rounded at tips, in order of decreasing length, 3, 2, 4, 1; body slightly swollen at midlength; costal folds 10, shallow; hind limb decidedly heavier than fore limb, femur shorter than tibia; sole broad; toes flattened, rounded at tips, in order of decreasing length, 4, 3, 2, 5, 1; tail quadrate-oval in section at base, constricted just behind anus, compressed oval toward tip where rounded above and sharp-edged below, lateral furrows inconspicuous.

Lower jaw thin (as compared with *Aneides*); tongue thin, subtriangular in outline, anterior end pointed, greatest width about half that of mouth at angles of jaws, attached along midline for anterior two-thirds of length to floor of mouth; internal nares small, set in from lateral margin of jaw; maxillary and mandibular teeth numerous and minute, lining margins of jaws to angle of mouth; vomerine teeth on two long arcs, meeting medially, extending laterally to sides of upper jaw, convex border anteriorly touching posterior border of internal nares; parasphenoid teeth in two elongate patches juxtaposed anteriorly, diverging posteriorly, slightly separated from vomerine teeth; teeth on jaws, vomers and parasphenoids all small, slenderly conic, and slightly curved.

Surfaces of body generally smooth; palms and soles slightly roughened.

Color (in alcohol) of upper and lateral surfaces blackish (black in life), marked with numerous large and small irregular spots and blotches of dull yellowish brown, these up to 3×5 mm. on tail; adjacent spots sometimes confluent; eyelid chiefly yellow; undersurface of body, dusky yellowish brown.

MEASUREMENTS OF SPECIMENS OF *Ensatina croceater* FROM THE WEST SLOPE OF THE SIERRA NEVADA IN CALIFORNIA

M. V. Z. No.	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
5618[1]	Aug. —, 1915	63[4]	.....	18.4	12.0	4.6	3.4	20.0	6.8	28	....	....
7374[2]	Mar. 13, 1920	91	35	16.7	10.2	4.3	3.5	16.0	6.0	27	18.4	8.4
7370[2]	Mar. 5, 1920	115	46	18.0	11.7	4.4	3.8	21.0	7.7	37	21.0	9.3
7372[2]	Mar. 13, 1920	116	54	17.0	10.2	4.0	3.5	17.0	7.0	29	19.5	8.0
8245[3]	June 1, 1903	123	47	19.0	12.8	5.4	4.5	20.6	8.0	36	22.3	11.0
7368[2]	Mar. —, 1920	128	55	20.2	12.3	4.2	3.0	19.0	8.0	37	23.5	10.6

[1] 4 mi. sw. Nelson, 6500 ft., Tulare Co.
[2] North Fork, Madera Co.
[3] Giant Forest, 6000 ft., Tulare Co.
[4] Head-and-body only

History.—This species was originally described by Cope in 1867 from material said to have come from Fort Tejon, Kern County. Two specimens, formerly in the collection of the Department of Zoology of the University of California and now in the Museum of Vertebrate Zoology (nos. 8243, 8244), which were originally contained in one bottle and labeled Ft. Tejon were considered by Grinnell and Camp (1917, p. 132) as the probable types of this species. There is no associated evidence to indicate this. The original description mentions a specimen, no. 4701 [U. S. National Museum], with John Xantus as the collector; so far as I know none of his material ever reached Berkeley. Van Denburgh (1916, p. 220) indicates that no trace of the type could then be found in the National Museum collection and Dr. Leonhard Stejneger is quoted as saying that it has not been there in his time [since 1889?]. More than this, Lockington (1880, p. 295) quotes Cope as saying (some time between 1876 and 1880) that the specimen reported from northern Lower California was then "the only one now known to be extant."

Range.—The exact area occupied by this species is still in doubt. It seems to be a form confined to the western flank of the Sierra Nevada. It has been recorded definitely north to Alta, Placer County, 3600 feet (Grinnell and Camp, 1917, p. 134), in Eldorado County (Stejneger and Barbour, 1917, p. 14), in Yosemite Valley, 4000 feet (two specimens in Mus. Vert. Zool.), at North Fork, Madera County, 3000 feet, and Dalton River, Fresno County (Mus. Vert. Zool.), Giant [not Grant] Forest, Sequoia National Park, 6000 feet, and 4 miles southwest of Nelson, Tulare County, 6300 feet (Grinnell and Camp, *loc. cit.*). There are records for three stations to the south of those mentioned, all of which need confirmation. These are Fort Tejon (Cope, 1867, pp. 210–211), "Cape St. [= San] Lucas, in Lower California, and . . . from near San Diego, at the northern end of that peninsula" (Cope, 1889, p. 151). Van Denburgh (1916, pp. 220–221) inquired into the basis of these southern records and finds the first "exceedingly dubious" and that the other two "need confirmation." He is undoubtedly correct in assuming that Cope's remark "I have seen one from near San Diego" refers to an individual reported by Lockington (1880, p. 295) as having been secured in Lower California, 75 miles southeast of San Diego, as Cope is said by Lockington to have passed upon the identification.

Life-history.—The specimens of *Ensatina croceater* from the Sierra Nevada collected in recent years have been found in situations similar to those occupied by *E. eschscholtzii* of the coast region, namely, under logs in the forest. No information is at hand concerning the breeding season. Young individuals have been collected as follows: Yosemite Valley, 4000 feet, June, 1921, total length 36 millimeters; North Fork and vicinity, 2750–3000 feet, Madera County, February 28, 1920, 39 millimeters; March 5, 1920, 42 millimeters.

Ensatina eschscholtzii Gray. Oregon Salamander

(Pl. 9, figs. 22, 23)

Ensatina eschscholtzii Gray (1850, p. 48). Original description, type from California [=Monterey; see Boulenger, 1882*b*, p. 54].

Heredia oregonensis Girard (1856, pp. 140–141). Type locality, Oregon.

Plethodon oregonensis, Cope (1869, p. 100).

Plethodon ensatus, Cope (1867, p. 167; see 1889, p. 150). [Not *Triton ensatus* Eschscholtz.]

Heredia oregonensis, Strauch (1870, p. 76). Monograph.

Plethodon oregonensis, Boulenger (1882*b*, pp. 54–55). General account.

Plethodon oregonensis, Cope (1883, p. 28). Locality records.

Plethodon oregonensis, Yarrow (1883, pp. 21, 155). Range.

Plethodon oregonensis, Cope (1889, pp. 148–150, text fig. 35). General account.

Plethodon oregonensis, Van Denburgh (1898, pp. 140–141). Breeding habits.

Plethodon oregonensis, Hubbard (1903, pp. 157–170, pl. 16). Habits; nature of poison glands.

Plethodon oregonensis, Esterly (1903, pp. 227–268, pls. 20–23). Poison glands.

Plethodon oregonensis, Ruthling (1915, p. 62). Occurrence in Santa Monica Mountains.

Plethodon oregonensis, Fowler and Dunn (1917, p. 26). Locality records.

Plethodon eschscholtzii, Grinnell and Camp (1917, p. 132, fig. 2). Range in California.

Plethodon eschscholtzii, Stejneger and Barbour (1917, p. 15). General range.

Ensatina eschscholtzii, Dunn (1923*a*, p. 39). Generic status.

Ensatina eschscholtzii, Stejneger and Barbour (1923, p. 12). General range.

Diagnosis.—Size moderate among California salamanders, total length up to 135 millimeters (5⅜ inches); naso-labial groove present; costal folds 10; temporal region flat; maxillary and mandibular teeth inconspicuous; tail compressed, slightly constricted at base, swollen at midlength; body coloration above plain dark red, ventral surface of body and feet orange or yellow.

Comparisons.—Distinguished from other California salamanders except Plethodontidae by presence of naso-labial groove and parasphenoid teeth; from *Batrachoseps* by larger size, stouter form, presence of 5 digits on hind foot, 10 instead of 15 or more costal folds, and reddish instead of blackish body coloration; from species of *Aneides* by 10 instead of 12 costal folds, smaller size of maxillary teeth, double curved pattern of vomerine teeth, flat instead of swollen temporal region, and unspotted pattern of coloration; from *Plethodon elongatus* by 10 instead of 15 costal folds, and absence of mid-dorsal stripe of light color along back; from *Ensatina croceater* by uniform instead of spotted coloration.

Description.—Form moderate, head small, limbs well developed but slender, tail large; head narrowly oval in outline from above, flat and thin in profile; end of muzzle rounded, lower jaw nearly terminal; external nares small, nearly at tip of muzzle, internarial space about equaling interorbital space; naso-labial groove present; sides of muzzle slanting, no canthus rostralis; ante-orbital region slightly more than length of orbit; orbit rather small; width of interorbital space three-fifths or more of length of orbit; interorbital and postorbital regions entirely plane; outline of lower jaw narrowly oval; angle of jaw at posterior margin of orbit; gular fold thin, very pronounced, extending up on side of neck where joined to nearly straight groove proceeding posteriorly from behind orbit; free portion of upper arm exceeding forearm; palm short, narrow; digits well developed, slender, narrowed at ends, third longest, second slightly exceeding fourth, first decidedly short; mid-dorsal groove present in preserved specimens; costal folds 10, grooves well indicated; hind limb half again stouter than fore limb; free portion of femur equal to tibia; sole narrow; toes well developed, third and fourth nearly equal, second longer than fifth, first very short; tail oval at base, constricted just posterior to anus, conspicuously swollen at midlength, compressed oval in section, tapering to a compressed tip.

Tongue thin, broad, and flat, oval in outline, anterior end rounded, greatest width about two-thirds that of mouth at angles of jaws, attached medially to floor of mouth for anterior two-thirds of its length; maxillary and mandibular teeth small, rounded, numerous, extending nearly to angle of jaw; internal nares moderately large, set in from margin of jaw; vomerine teeth in two long arcs, meeting medially, extending laterally nearly to margin of upper jaw, convex anteriorly where nearly reaching posterior margin of internal nares; parasphenoid teeth in two distinct patches, juxtaposed anteriorly, divergent and separated posteriorly.

Surfaces of body everywhere smooth; palms and soles slightly roughened.

Coloration (in life) above dark red, without spotting; ventral surface and tips of digits, pink or pale red; (in alcohol) upper surface variously bluish black or dark reddish brown, undersurface pale yellow or whitish.

History.—This species was originally described by Gray in 1850 from a specimen collected at Monterey, being called *Ensatina esch-*

scholtzii. This name was confused in his mind with that of *Triton* [= *Dicamptodon*] *ensatus*, in consequence of which the name *Heredia* [= *Plethodon*] *oregonensis* given by Girard in 1856 was used for a long time to designate the species. Boulenger showed in 1882 that the specimen upon which the name *eschscholtzii* was based actually came from Monterey and was a *Plethodon,* although he continued the use of Girard's name. Grinnell and Camp (1917, p. 132) were first to use the present specific designation. Dunn (1923*a,* p. 39) states, as a result of studies on the entire family Plethodontidae, that the species *eschscholtzii* (and *croceater*) should be separated from *Plethodon* and placed in the genus *Ensatina* Gray 1850. He includes here, as well, *Urotropis* [= *Ensatina*] *platensis*, the only salamander known from southern South America, which inhabits the vicinity of La Plata.

MEASUREMENTS OF ADULT SPECIMENS OF *Ensatina eschscholtzii* FROM CALIFORNIA

M.V.Z No.	Sex	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbita space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4473	..	Near Sierra Madre at 2500 ft., Los Angeles Co. ..	Aug. 9, 1912	99	43	17 0	9 7	4 0	3 0	17.0	7.1	26	19.0	10.2
4947		6 mi. w. Inverness, Marin Co. .. .	June 4, 1913	105	42	16.6	9.7	3.7	3.7	19.0	7 5	31	20.7	10 0
9148	♀	Carlotta, Humboldt Co...	July 26, 1923	110	48	16.6	10.2	3 8	3 3	17 2	6.6	32	19 0	8.8
2376	.	Muir Woods, Marin Co. ..	Mar. 5, 1910	114	57	17 6	9 0	5.0	3.0	16.5	6 7	25	20 0	9.2
2382	♀	Berkeley, Alameda Co. ...	Mar. 12, 1910	117	46	19 5	11 0	5 3	3.7	20 0	8 3	32	22.5	11.0
4890	....	Forest Home, 5200 ft., San Bernardino Co.	Aug. 16, 1913	135[1]	71[1]	....	12 3	4 5	3 6	21 7	8.0	31	23.7	11.8

[1] Specimen broken, measurements approximate.

Range.—*Ensatina eschscholtzii* occupies the longest extent of territory of any of the Pacific Coast Plethodontidae. At the north it has been recorded from Discovery Harbor, Puget Sound, Oregon [= Washington] (Girard, 1858, pp. 11–13), at South Bend, Pacific County, and Hoquaim and Quiniault, Chehalis County, Washington, and at Marshfield, Coos County, and Harbor and Port Orford, Curry County, Oregon (specimens in Calif. Acad. Sci.). In California it has been found (Calif. Acad. Sci.) at the north near Crescent City and at Requa, Del Norte County, and at Sweet Briar, Shasta County; Strawberry, Eldorado County, is the southernmost [and only?] record in the Sierra Nevada. It is common in the Coast Ranges east-

ward to Agua Caliente, Sonoma County (Calif. Acad. Sci.), and at Berkeley (Mus. Vert. Zool.). To the south no records are known between Monterey (Gray, 1850, p. 48) and Carmel (Calif. Acad. Sci.) in Monterey County, and Los Angeles County. Ruthling (1915, p. 62) has recorded the species from Topanga Cañon, Santa Monica Mountains, and it is present in the San Gabriel Range, as about Sierra Madre (Mus. Vert. Zool.), and in Palmer's Cañon near Pomona (specimen in Pomona College Museum). One individal was taken in a quarry in the foothills ten miles northwest of San Bernardino (Mus. Vert. Zool.); and one at Forest Home, San Bernardino Mountains, altitude 5200 feet, marks the known southern limit of range (Grinnell and Camp, 1917, p. 132). The California Academy of Sciences has specimens from Castle Rock, 3 miles north of Crescent City, and from Whale Rock in the harbor of that city.

Life-history.—*Ensatina eschscholtzii* may be described as a 'typical' Plethodont salamander, showing no conspicuous specialization in structure or habits (with the possible exception of the tail). So far as known this species is strictly terrestrial. All of the specimens at hand were collected under objects resting on the surface of the ground or in the burrows of earth-dwelling rodents only a few inches below the ground surface. In common with other Plethodonts in central California *eschscholtzii* usually disappears from its surface haunts at the approach of the dry season and reappears soon after the first autumn rains. The nature of its aestival retreat is unknown save in a few instances where individuals have been found in rodent burrows. This species is rather less common than *Aneides lugubris;* at least, in the vicinity of Berkeley it is outnumbered by the latter species, and judging from the relative number of specimens of the two at hand from central and southern California the same condition holds rather generally. In the northwestern part of the State, however, *Ensatina eschscholtzii* appears to be more common.

In southern California *Ensatina eschscholtzii* is relatively uncommon. Camp (MS) says that, in Bailey Cañon near Sierra Madre, one was found at an altitude of about 1200 feet, in a tunnel entrance in the cañon bottom. Six others, seen at various times in the golden oak belt of the same cañon, at about 2300 feet altitude, were found in the following sorts of surroundings: (1) beneath a box in rather dry soil, (2) in a cellar beneath a cabin, (3) among wet leaves, (4) several inches below the ground surface in loose wet earth, (5) in a large hollow log (Camp, MS). The dates of these several observations are not mentioned.

The fortunes of a group of four adults and two young individuals which lived beneath boxes and boards in a grove of Pittosporum trees on the Berkeley campus were followed for a time in the winter of 1921–22. During the spring of 1921 all of the salamanders of this species, with possibly one exception, had been removed. None was seen during the dry summer period, but with the first autumn rains several individuals of *eschscholtzii* appeared. Repeated daytime examinations during November and December showed that the animals made frequent changes of location. On one day they would be under a large box beside a building; on another occasion they would be found out under boards, 20 feet away but still in the leaf mat under the trees. The young moved about in the same way as the adults. Evidently any convenient shelter served as harbor for the animals during the day, their restriction to the general neighborhood being brought about by the zone of harder and drier ground outside the grove and also by the lack of shelter in that direction.

The box which furnished the principal shelter for the salamanders was removed on January 24, 1922, up to which time the animals had been present continuously; thereafter they could not be found. Another box placed in the same location a day or two later failed to attract any salamanders. This suggests that the original population comprised the only individuals of *eschscholtzii* present in the grove, and that when their principal daytime shelter was removed the animals made a permanent change of base, after which they did not return to their former haunt.

Captive specimens when handled sometimes stand up high on their toes. When handled roughly by grasping the head or body the tail is apt to be swept around laterally—alligator fashion—and at the same time the glands on the tail begin to secrete a colorless fluid. This species displays some agility in movement; when dropped from the hand an individual usually manages to turn during the course of the descent so as to alight on the feet, or at least on the ventral surface.

Van Denburgh (1898, pp. 140–141) was first to report the breeding habits of this species. A female, with three eggs, was found under a decayed log in the redwoods at Mill Valley, Marin County, April 19, 1896. The salamander and eggs were placed with bits of wood and damp moss in a darkened jar. The female at once took charge of the eggs,

> . . . lying beside them and holding them in a loop of its tail. Evidently dissatisfied with their position and surroundings, the Plethodon [=*Ensatina*] moved the eggs from place to place in the jar, holding them always in the crook of its

tail. This was done several times in the course of three or four days, and the solicitousness of the salamander continued until the eggs were quite moldy. Finally the eggs of the cluster were broken apart and one was eaten by the salamander (Van Denburgh, 1898, p. 140).

A female taken in a cañon [probably Strawberry], at Berkeley, February 9, 1904, contained 23 ova which now (1924) measure 4.5 to 4.7 millimeters in diameter. Another obtained at Berkeley, March 12, 1910, contains ova 5.7 millimeters in diameter.

During excavation of a tunnel system of the rodent, *Aplodontia rufa phaea,* in the hills three miles west of Inverness, Marin County, on June 4, 1913, two individuals of *Ensatina eschscholtzii* were found in one of the underground compartments. With the salamanders there was a group of 13 'white' eggs. According to the field notes (C. L. Camp, notebook in Mus. Vert. Zool.) the larger of the two salamanders "seemed very much bloated and almost transparent when taken. As I held it in my hand it emitted about ¼ oz. of clear odorless liquid and became normal in size." These eggs after preservation in alcohol measure 5.5 to 5.75 millimeters in diameter and the outer jelly coat 5.9 to 7.5 millimeters (pl. 9, fig. 22).

At Carlotta, Humboldt County, on July 26, 1923, Dr. Joseph Grinnell found two adult individuals, each in attendance upon a cluster of 16 eggs. They were under slabs of redwood on the ground. The eggs are in what would appear to be relatively early stages of development. The head-and-body and the limb buds are formed. Each embryo is coiled on the surface, apparently a meroblastic type of development like that characteristic of birds and in contrast to the mode of development in aquatic spawning Caudata and Salientia. The eggs measure 5.0 to 5.5 millimeters in diameter (across the yolk mass) and the outside of the apparently single jelly coat is 7.6 to 7.8 millimeters in diameter (pl. 9, fig. 23). The embryo fits closely into the vitelline capsule. When found, the eggs were nearly transparent; preservation has made the yolk mass opaque while the jelly coat remains clear.

I am unable to see that these eggs are definitely peduncled as is the case with eggs of both *Batrachoseps attenuatus* and *Aneides lugubris.* The eggs of *Ensatina eschscholtzii* here described seem to have come in contact with a substratum to which they adhered, and adjacent eggs are attached to one another. But this seems to have been due merely to the viscid nature of the jelly coat at the time of extrusion.

The growth of *eschscholtzii* is indicated by the following. The smallest individuals taken between March and September measure 44.5 to 57 millimeters in length; a second group includes two each measuring 77, 83, and 92 millimeters, respectively. Above the latter are single individuals, 99, 105, 110, 114, 117, and 135 millimeters in total length. These suggest that three years are required to attain a length of about 100 millimeters and exceptional individuals (four or more? years of age) reach a size of 135 millimeters.

Hubbard (1903, pp. 157–170) has made a study of this species (under the name *Plethodon oregonensis*) with particular attention to the function of the glandular swollen tail. *Eschscholtzii* has on the dorsal and lateral surfaces of the tail numerous large gland cells which produce an acid non-mucous astringent secretion. When the salamander is irritated as by attack on the part of an enemy such as a snake, the milky secretion of these glands is poured forth. Snakes which have eaten or attempted to eat salamanders of this species have been seen to gape for some time afterward, indicating that something, presumably the secretion of these glands, was distasteful.

The tail of *eschscholtzii*, besides being swollen at midlength, bears a definite constriction a short distance behind the anal opening. Under stress of unfavorable circumstances an autotomous sluffing of the tail occurs by a simple separation of adjacent vertebrae at this constriction.

Upon the basis of experimental attempts to feed specimens of *eschscholtzii* to two species of snakes (*Thamnophis* sp. and *Diadophis amabilis*), Hubbard concludes that the tail glands of the salamander offer partial protection to the animal. The experiments, however, do not seem to me to be conclusive. So far as the published data indicate, only four specimens of *eschscholtzii* were used. Two young individuals without tails were eaten by a garter snake; one large individual with tail detached was eaten *tail and all* by a *Diadophis*, which on the next day, after one attempt, declined to feed on another *Ensatina*. I am unable to agree that a *Diadophis* after having eaten a specimen of *Ensatina eschscholtzii* the day previously would be hungry, and I think that satiety upon the part of the snake rather than repulsion by the glandular secretion from the tail of the salamander is an equally possible, and even more highly probable, explanation of the snake's refusal to feed.

Hubbard's concluding paragraphs are as follows:

To summarize the results of the experiments: We have, in these three species, a graduated series so far as the relation of the power of autotomy and the presence of these poison glands are concerned. Batrachoseps yields comparatively little poisonous secretion when stimulated; Plethodon yields it abundantly on the tail and Diemyctylus pours it out very generally over the dorsal surface of the body. Batrachoseps is eaten with avidity by snakes. Plethodon is not rejected, but Diemyctylus seems not to be taken at all as food. In Batrachoseps, where the secretion is slight, autotomy occurs on *little provocation and at almost any point.* In Plethodon, where the secretion is restricted to the tail though abundant there, autotomy occurs only as a last desperate resource and but in one region. In Diemyctylus where the secretion is copious and general over the body autotomy does not take place.

Finally, passing from the region of fact and entering that of hypothesis, it seems fair to conclude that we have in these three species a case of adaptive correlation between autotomy and protective secretion. Batrachoseps appears to have, in its great tail-shedding power, some compensation for its limited defensive glands. Diemyctylus has no need of this, being sufficiently safe, so far as one means of defense is concerned, in its own abundant secretion. And, finally, it seems probable that when its tail secretion fails the Plethodon, this species sheds that organ to supplement the inadequacy of poison.

Hydromantes platycephala (Camp). Mount Lyell Salamander

Spelerpes platycephalus Camp (1916*b*, pp. 11–14, figs. 1–5). Original description, type from head of Lyell Cañon, 10,800 feet, Yosemite National Park, California.

Spelerpes platycephalus, Grinnell and Camp (1917, p. 132, fig. 2). Range.

Eurycea platycephala, Stejneger and Barbour (1917, p. 20). Range.

Lyell Salamander, Grinnell and Storer (1921, p. 178). Occurrence.

Hydromantes platycephalus, Dunn (1923*a*, p. 40). Relationships.

Hydromantes platycephala, Stejneger and Barbour (1923, p. 17). Range.

Eurycea platycephala, Grinnell and Storer (1924, p. 652, pl. 60*f*). General account of discovery.

Diagnosis.—Size moderate among California salamanders, total length up to 99.4 millimeters (4 inches); naso-labial groove present; head depressed, breadth about three times greatest thickness; interorbital space greater than length of orbit; costal folds 12; digits half-webbed; parasphenoid tooth patches separated medially; tongue attached only by central pedicel, freely protrusible.

Comparisons.—Distinguished from other California Caudata except Plethodontidae by presence of naso-labial groove and of parasphenoid teeth; from Plethodontidae in general by depressed form of head, separated patches of parasphenoid teeth, and presence of half-webs between the blunt digits.

Description (based on type and cotype, nos. 5693 ♀, 5694 ♂, Mus. Vert. Zool.).—General form and especially head, depressed; muzzle truncate oval in outline from above, thin and evenly rounded in profile; lower jaw overhung by muzzle; no canthus rostralis; external nares very small, terminal; length of muzzle equal to orbit; orbit large; interorbital space flat, its width greater than length of orbit;

greatest width of head more than that of body; neck constriction slight; lower jaw broadly oval in outline; gular fold at middle of neck; limbs moderate; upper arm slender; forearm stouter and shorter than upper arm; palm rounded, without tubercles; digits short, subequal, third longest, first shortest, tips slightly expanded; interdigital webs extend about half length of digits; body depressed, not appreciably enlarged at middle; costal folds 12, not clearly indicated; hind limb resembling fore limb, but slightly longer; exposed portion of femur slightly longer than tibia; sole of foot broader than long, smooth; toes subequal, inner one smallest, tips slightly dilated; webs about half length of toes; tail about one-third total length, cylindric at base, tapering evenly to tip. Surfaces everywhere smooth.

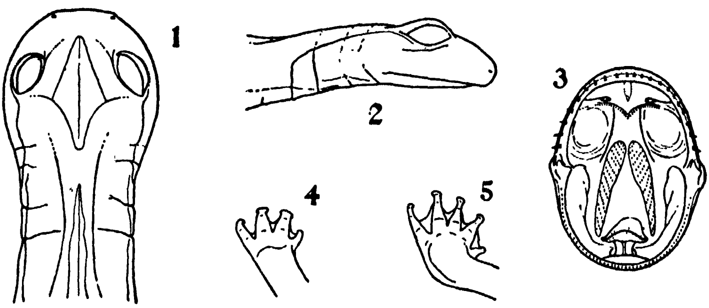


Fig. NN. *Hydromantes platycephala*, × 2⅓ (after Camp, 1916*b*, figs. 1–5).

1. Top of head, ♀ (no. 5693, M. V. Z.). Note breadth of head and width of interorbital space.
2. Side of head, ♀ (no. 5693, M. V. Z.). Note small external naris, thin form of head, relative size of eye.
3. Opened mouth, ♂ (no. 5694, M. V. Z.). Note long maxillary teeth, double arc of vomerine teeth, divergence of parasphenoid teeth and pediceled tongue.
4. Left forefoot, ♂ (no. 5694, M. V. Z.).
5. Left hind foot, ♂ (no. 5694, M. V. Z.).
   Note extent of webbing, and short blunt form of toes.

Tongue small and thin, less than half width of head, oval in outline, free all around and pedunculate, freely protrusible; maxillary teeth short and numerous and confined to anterior portion of jaw in female, longer, less numerous, protruding below closed lips, and continued to angle of jaw in male; vomerine teeth entirely posterior to internal nares, in two arcs joined medially and extending laterally beyond internal nares; parasphenoid teeth in two elongate patches slightly separated anteriorly, divergent posteriorly.

"Color in life dark chocolate, marked evenly and thickly on back and sides of head and body, on limbs, feet and tail, and below chin, with lichen-like gray markings, yellowish in tinge down middle of back, where less distinct, and bluish on sides; underparts posterior to gular fold uniform dark chocolate. Iris bright yellow. In alcohol the yellowish tints have disappeared" (Camp, 1916*b*, p. 13).

MEASUREMENTS OF TWO SPECIMENS OF *Hydromantes platycephala* FROM LYELL CAÑON, YOSEMITE NATIONAL PARK

(Dimensions in millimeters)

	Mus. Vert. Zool. No.		
	5693, ♀		5694, ♂
	(alive)	(in alcohol)	(in alcohol)
Total length	106.5	99.4	86.9
Length of tail	35.5	33.6	28.7
Snout to gular fold	15.3	14.2	12.6
Greatest width of head	11.9	9.5	10.2
Orbit	....	3.6	3.7
Interorbital space	....	4.0	4.1
Foreleg	16	15.5	15.5
Hand	.....	6.0	4.8
Hind leg	18	17.0	16.9
Hind foot	. .	7.0	7.0

Range.—This species was discovered on July 18, 1915, when two specimens were taken in the head of Lyell Cañon on the slopes of Mount Lyell, in Yosemite National Park. The locality of capture (and only known record station to date) was

> about a mile from the [Lyell] glacier and a little below timber line, here marked by a few stunted white-bark pines [*Pinus albicaulis*] on the tops of the ridges. The exact spot was at the 10,800-foot contour, on a steep, east-facing hillside above the Donohue Pass trail in a small patch of heather [*Phyllodoce Breweri*]. A stream close by issued directly from the snow banks and disappeared beneath rock-slides below. The two specimens were found to have been captured simultaneously in a spring-clip mouse-trap set in front of a small hole running into the moist soil beneath some rocks (Camp, 1916*b*, pp. 13–14).

Life-history.—Nothing is known concerning the life of this boreal salamander of the Sierra Nevada. The sole station of record is in the upper part of the Hudsonian Zone. *Bufo canorus,* another local species, and *Hyla regilla,* which ranges over most of the Pacific Coast, are the only amphibian associates of *platycephala.* The webbing of the digits suggests some degree of aquaticity in habits.

"*Spelerpes platycephalus*" was compared by Camp (1916*b*, p. 12) with *Spelerpes leprosus* Cope from northeastern Mexico, but Dunn (1923*a*, p. 40) places it in the genus *Hydromantes* Gistel, of which there are two other species, *H. genei* (Schlegel) and *H. italicus* Dunn (*H. fuscus* Bonaparte), in Europe.

Aneides ferreus Cope. Rusty Salamander

Anaides ferreus Cope (1869, pp. 109–110). Original description, type from Fort Umpqua, Douglas County, Oregon.

Autodax ferreus, Van Denburgh (1916, p. 216). General range, including California.

Aneides ferreus, Grinnell and Camp (1917, p. 135, fig. 2). Range in California.

Aneides ferreus, Stejneger and Barbour (1917, p. 21; 1923, p. 18). General range.

Diagnosis.—Size small, total length of adults up to 120 millimeters (4¾ inches); naso-labial groove present; inner digit on each foot rudimentary; tail rather slender; costal folds 12; coloration 'marbled,' less often spotted.

Comparisons.—Distinguished from other California salamanders except Plethodontidae by presence of naso-labial groove; from *Batrachoseps, Ensatina,* and *Plethodon* by 12 costal folds; from *Aneides lugubris* ssp. and *Aneides flavipunctatus* by rudimentary inner digit on each foot, and 'marbled' pattern of coloration.

Description (based upon adults in collection of California Academy of Sciences).—Size moderate among Plethodontidae; head large, body slender, digits proportionately large; head trapezoidal in outline from above, muzzle square-ended; muzzle slanting in profile, rounded at tip, completely overhanging lower jaw; external nares terminal; naso-labial groove minute, proceeding from lateral margin of naris; canthus rostralis rounded; orbit large, lorger than canthus rostralis; inter-orbital space flat, its width less than length of orbit; temporal region swollen, rising above level of upper eyelid; posterior portion of commissure of jaw bent upward toward swollen temporal region; greatest width of head behind angle of jaw, and more than distance from tip of snout to angle of mouth; lower jaw acutely oval in outline; gular fold distinct, at middle of neck region; fore limb moderate; exposed portion of upper arm equaling forearm; hand slightly exceeding forearm in length; palm smooth; inner (first) digit rudimentary; third longest, second and fourth about equal; all digits square-ended; a fine mid-dorsal groove on back; costal folds 12; hind limb longer and slightly stouter than fore limb; exposed portion of femur slightly longer than tibia; foot longer than tibia; sole smooth; toes in order of decreasing length 4, 3, 5, 2, 1, innermost rudimentary as on palm; toes square-ended; tail slender, circular in cross-section at base, compressed but not thin at tip. Surface of body everywhere very smooth.

Tongue broad, practically filling floor of mouth, thin, broadly attached; internal nares relatively large, placed back from end of snout and well in from margin of jaw; vomerine teeth in broadly V-shaped arrangement between internal nares, 5 or 6 teeth on each side; parasphenoid teeth in one patch, narrower anteriorly; maxillary teeth few, well developed.

Color (in alcohol) above dark reddish brown; 'marbled' pattern of light yellowish brown on dorso-lateral portions of body; undersurface everywhere dusky yellow, with numerous fine (0.5 mm.) dots of clear yellow.

Remarks on coloration.—The southernmost series of specimens, from Comptche, Mendocino County (nos. 28499–28506, Calif. Acad. Sci.), presents a pattern of fine yellow dots on the dorsal as well as the ventral surface, and the 'marbled' pattern seen in the more northern individuals is indicated chiefly along the sides of the body in the largest (oldest?) specimen. The mid-dorsal region in all specimens tends to be dark without light patterning. The variegated pattern extends to the end of the tail in northern specimens and the fine spotting is continued to the tip of the tail in the Comptche material.

MEASUREMENTS OF ADULT SPECIMENS OF *Aneides ferreus* FROM CARLOTTA, HUMBOLDT COUNTY, CALIFORNIA, COLLECTED JULY 26, 1923

M. V. Z. No.	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
9156	99	40	15.	9.0	3.5	2.0	15.5	6.0	31	17	8.7
9157	104	45	14.7	9.7	3.8	2.3	15.3	7.5	29	18	9.0

Range.—This salamander is found in the coastal district of California from Comptche, Mendocino County (Van Denburgh, 1916, p. 216), north to the Oregon boundary. The California Academy of Sciences has specimens from Carlotta, Alton, Trinidad, and Orick, Humboldt County, and Requa, Del Norte County. In Oregon it has been taken at Fort Umpqua (Cope, 1869, pp. 109–110) and at Elmira, Lane County (Calif. Acad. Sci.). No specimens are known from Washington, but Yarrow (1883, p. 159) lists two from "Puget's Sound, Oreg.," not mentioned by Cope. It has been taken at Union Bay, Bayne Island, British Columbia (Calif. Acad. Sci.). All the localities of record are within 50 miles of the sea coast.

Life-history.—Practically nothing is known of the habits of *Aneides ferreus.* Van Denburgh (*loc. cit.*) says that two specimens obtained at Requa, May 22–26, 1911, "were taken from the rotten wood of a dead tree in which they were living some 20 feet above the ground." This suggests that *ferreus* may be, like *lugubris,* of arboreal habitat. The former has the ends of the digits rather square-ended, as though tending toward development of expanded tips such as are seen in climbing amphibians like the Hylidae. Two specimens of *ferreus* were taken under slabs of redwood on the ground in a virgin

redwood forest near Carlotta, Humboldt County, on July 26, 1923 (nos. 9156, 9157, Mus. Vert. Zool.). Numerous specimens of *Batrachoseps attenuatus*, *Ensatina eschscholtzii*, and *Triturus torosus* were found in the same locality.

There are two young specimens in the collection of the California Academy of Sciences: No. 29067, Trinidad, Humboldt County, May 18, 1911, measures 33 millimeters in total length, and no. 28502, Comptche, Mendocino County, April 27–30, 1911, is 34 millimeters long. These either overwintered as exceptionally small individuals or, if but recently hatched, indicate that the breeding season of *ferreus* is earlier in the year than with the other two mainland members of the genus.

The next size-group above the two individuals mentioned is about 60 millimeters in total length.

Aneides flavipunctatus (Strauch). Black Salamander

Plethodon flavipunctatus Strauch (1870, pp. 71–72). Original description, type from New Albion [probably the coastal portion of Sonoma County], California.

Plethodon flavipunctatus, Boulenger (1882*b*, pp. 55–56).

Plethodon iëcanus Cope (1883, pp. 24–25). Type locality, Baird, Shasta County, California.

Aneides iëcanus, Cope (1886, p. 526). Generic allocation.

Plethodon iëcanus, Townsend (1887, pp. 240–241).

Plethodon flavipunctatus, Cope (1889, p. 145).

Autodax iëcanus, Cope (1889, pp. 187–189, text fig. 46). General account.

Autodax iëcanus, Van Denburgh (1895*b*, pp. 776–778). Range; breeding habits; eggs.

Autodax iëcanus, Ritter and Miller (1899, p. 696).

Plethodon flavipunctatus, Van Denburgh (1916, p. 221).

Aneides iëcanus, Grinnell and Camp (1917, pp. 135–136, fig. 2). Range.

Aneides iëcanus, Stejneger and Barbour (1917, p. 21; 1923, p. 18). Range.

Diagnosis.—Size small among California salamanders, total length up to 97 millimeters ($3\frac{7}{8}$ inches); temporal muscles swollen (small in young); maxillary and mandibular teeth enlarged; costal folds 12; distal portion of tail strongly compressed; general coloration black, with few fine white dots chiefly on lateral and lower surfaces of body.

Comparisons.—Distinguished from other California salamanders except Plethodontidae by presence of naso-labial groove; from *Batrachoseps* [which it resembles in some respects] by presence of 5 digits on hind foot, by 12 instead of 15 or more costal folds, by compressed form of tail, by absence of reddish stripe along back, and by presence of small white spots on body; from *Ensatina* by 12 instead of 10 costal folds, larger maxillary and mandibular teeth, and black coloration; from *Aneides lugubris* ssp. and *A. ferreus* by more slender body, compressed form of tail and black instead of dark red body coloration.

Description (based on nos. 4124 and 8258, Mus. Vert. Zool.).—General form slender, head moderate, limbs well developed, tail large, compressed; head trapezoidal or truncately oval in outline from above; muzzle thin, rounded at tip, overhanging lower jaw; external nares terminal, directed anteriorly; naso-labial groove minute; anteorbital region rounded, slightly shorter than length of orbit; orbit moderate; interorbital region nearly or quite equaling length of orbit; temporal region swollen in adult, with median furrow extending forward to interorbital space; angle of jaw well behind posterior margin of orbit; margin of upper jaw nearly straight; lower jaw rounded or acutely oval in outline; chin region flat; gular fold conspicuous, extending up side of neck, and nearer insertion of fore limb than angle of jaw; fore limb slender; free portion of upper arm shorter than forearm; palm slightly longer than wide; digits short, blunt-ended, with slight webs between bases, third longest, second and fourth subequal, first very short; body nearly straight-sided; costal folds 12; hind limb decidedly stouter than fore limb; femur and tibia both short, nearly equal in length; sole slightly longer than wide; toes short, blunt-ended, with minute webs between bases, in order of decreasing length 4, 3, 5, 2, 1, innermost toe very small; tail subquadrate at base, strongly compressed toward tip, with numerous vertical furrows on sides.

Tongue cuneiform, thin, filling about two-thirds of width of mouth, broadly attached along midline to floor of mouth; internal nares well separated, slightly inside of margin of mouth; maxillary and mandibular teeth enlarged, but more slender and curved than in *A. lugubris;* vomerine teeth 3 (or 4) on each side, posterior to and mediad of internal nares, in broadly V-shaped arrangement, the two rows separated medially; parasphenoid teeth in two narrow parallel patches, well separated medially, about 5 lengthwise rows of teeth in each patch.

General coloration (in alcohol) uniform bluish black; chin, margin of gular fold, spots at axilla and groin, and plantar surfaces of feet, dull yellow; dorsal and lateral surfaces (of no. 4124) with scattered fine dots of white.

MEASUREMENTS OF SPECIMENS OF *Aneides flavipunctatus* FROM MENDOCINO COUNTY, CALIFORNIA

M. V. Z. No.	Sex	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
4126[1]	....	Nov. 10, 1912	85	40	13.4	7.0	2.8	2.4	10.6	4.7	23	12.5	4.6
4125[1]	....	Nov. 10, 1912	88	38	13.0	7.3	3.2	2.6	11.3	4.5	25	13.6	6.0
4124[1]	....	Nov. 10, 1912	97	40	14.0	8.4	3.5	3.0	12.0	4.7	31	13.3	6.1
8258[2]	♀	July 1, 1913	69[3]	....	16.2	10.4	3.4	3.4	13.8	5.2	35	16.3	8.8

[1] Ukiah.
[2] Laytonville.
[3] Head-and-body only.

History.—The previous disposition of Strauch's *Plethodon flavipunctatus* has never been satisfactory. Boulenger (1882*b*) and Cope (1889) both included it as a separate species, without comment. Van Denburgh (1916) dismissed it with the remark "I have no doubt that this is the same species as Cope's *Plethodon croceater,* with which the description agrees." I was earlier of the same opinion, misled by the coloration indicated by the specific name, and by failure to study carefully the exact wording of Cope's description (which was copied from a translation in Boulenger's *Catalogue*). Recent access to Strauch's original description has reopened the problem, a critical study showing that Strauch undoubtedly had specimens of the species which Cope in 1883 described as *Plethodon ïëcanus.* Important features in the description which indicate this are the form of the head, the furrow on the crown, the form of the palatine (vomerine) teeth, the number of costal furrows, the coloration, and the compressed end of the tail. Strauch's comparison of *flavipunctatus* with *Plethodon glutinosus* lends further strength to the position that *flavipunctatus* and *ïëcanus* are identical, as "*ïëcanus*" bears a close resemblance to *glutinosus* in general external appearance. This species should henceforth be designated as *Aneides flavipunctatus* (Strauch).

In view of the fact that the original description is relatively inaccessible, I give it here *verbatim.*

53. *Plethodon flavipunctatus* n. sp.

Die überaus reiche herpetologische Ausbeute, welche Hr. Conservator Wosnessensky während seines mehrjährigen Aufenthaltes in Californien zusammengebracht hat, enthielt auch drei Exemplare einer Molch-Art, welche dem *Plethodon glutinosus* Green sehr nahe steht, von demselben aber in der Stellung der Gaumenzähne durchaus abweicht, und welche ich daher für neu erklären muss. Diese neue Art, der ich den Namen *Plethodon flavipunctatus* beigelegt habe, erinnert zwar in der Färbung und Zeichnung an *Ambystoma punctulatum,* welches Gray sehr kurz charakterisirt hat und von welchem er später selbst sagt, dass es "nearly allied to the genus Plethodon" sei, dürfte aber doch wohl schwerlich mit demselben identisch sein, da die Gray'sche Art einen comprimirten Schwanz und eine weiss gefärbte Unterseite besitzt, während bei dem gleich zu beschreibenden *Plethodon* der Schwanz, bis auf die äusserste, leicht comprimirte Spitze volkommen drehrund ist, und die Unterseite eben so dunkel gefärbt erscheint, wie die Oberseite.

Der Kopf, der ziemlich lang und in der Mitte des Scheitels mit einem mässig tiefen Längseindrucke versehen ist, zeigt in der Gegend der Mundwinkel die grösste Breite, verschmälert sich nach hinten in ziemlich auffallender Weise und läuft auch in eine recht spitz zugerundete Schnauze aus. Die Zunge ist auffallend gross, sehr dünn, blattförmig, unterscheidet sich aber in der Form kaum von der Zunge der *Plethodon glutinosus* Green, die Gaumenzähne dagegen haben eine

Note.—Dr. E. C. Van Dyke (MS) states that M. Wosnessensky was in California in 1840 and 1841 and collected mainly at old Fort Ross, Sonoma County, at New Helvetia [= Sacramento], on Mount Saint Helena, and at San Francisco.

durchaus abweichende Stellung; während nämlich bei der eben genannten Art die beiden Gaumenzahnreihen nach hinten unter sehr stumpfem Winkel convergiren und zusammengenommen eine schwach winklig gebogene, in der Mitte unterbrochene Querreihe darstellen, deren äussere Enden den Hinterrand der inneren Nasenöffnungen bilden, beginnen bei *Plethodon flavipunctatus* die in Rede stehenden Zahnreihen, die ausserdem auch um ein Drittel etwa kürzer sind, an der hinteren inneren Ecke der jederseitigen inneren Nasenöffnung, laufen schräge nach hinten und innen gegen einander, ohne sich jedoch mit ihren hinteren Enden zu berühren, und schliessen somit zusammen einen Winkel ein, der etwas kleiner ist als ein Rechter. Der Rumpf ist cylindrisch, an der Unterseite etwas abgeflacht, längs der Vertebrallinie vertieft und an den Seiten mit 13 tiefen Hautfalten versehen, von denen die letzte nicht ganz deutiich [sic] ausgebildet ist. Der Schwanz ist länger als der Rumpf, an der Basis etwas abgeflacht, im weiteren Verlaufe drehrund und nur an der Spitze leicht comprimirt; das Ende desselben ist sehr scharf zugespitzt, und in seinen beiden vorderen Dritteln besitzt er deutliche verticale Hautfalten, welche ihm ein geringeltes Ansehen verleihen. Die Extremitäten stimmen mit denen des *Plethodon glutinosus* [p. 72] Green vollkommen überein, nur sind die Zehen durchweg schlanker, weniger abgeflacht und mehr zugespitzt.

Die von Epidermis entblössten Stücke sind überall tief schwarz gefärbt und mit recht grossen, unregelmässig geformten und gestellten weisslichen Makeln verziert; diese Makeln sind an den Seiten des Kopfes und Rumpfes, so wie auf der Oberseite des Schwanzes viel zahlreicher als auf dem Rücken, erscheinen am Bauche und an der Kehle kleiner und weniger zahlreich und fehlen auf der Oberseite des Kopfes und an der Unterseite des Schwanzes gänzlich. Bei einem der drei mir vorliegenden Exemplare, bei welchem sich die Epidermis stellenweise erhalten hat, sind die Makeln an den mit Oberhaut versehenen Stellen sehr hell bräunlichgelb und die Grundfarbe sehr dunkel bräunlichgrau.

Maasse. Totallänge des Thieres 11,7; Länge des Kopfes 1,6; Länge des Rumpfes 4,8; Länge des Schwanzes 5,3; Länge der Vorderextremität 1,4; Länge der Hinterextremität 1,7; Länge der Mittelzehe an den Hinterfüssen 0,4; Breite des Kopfes in der Gegend der Mundwinkel 1; Dicke des Schwanzes an der Basis 0,6; Höhe desselben an derselben Stelle 0,5.

Habitat. Californien (Neu-Albion). (Strauch, 1870, pp. 71–72.)

Range.—This species has been found at Sweet Briar Camp (Calif. Acad. Sci.) and Baird, Shasta County (Townsend, 1887, pp. 240–241; Cope, 1889, p. 189); in Humboldt County, and at Ukiah (Grinnell and Camp, 1917, p. 135), and Comptche, Mendocino County; and at Skaggs Springs, and Camp Meeker, Sonoma County (Calif. Acad. Sci.). The latter is the southernmost record north of the Golden Gate. To the south, the species is reported at Mountain View (Grinnell and Camp, 1917, p. 136), at Los Gatos and Stephens Creek, Santa Clara County, and at Glenwood and Boulder, Santa Cruz County (Van Denburgh, 1895*b*, pp. 776–778). Its range is, for the most part, inland from that of *Aneides lugubris.* It is worthy of note that all three mainland species of *Aneides—lugubris, flavipunctatus* and *ferreus*—have been found at Comptche, Mendocino County.

Life-history.—Van Denburgh has found this species in some numbers at Los Gatos, Santa Clara County, and has given an account of the habits of the species based on material from that locality. It has been seen abroad at late dusk on two occasions only. When moving it usually walks quite slowly, using one foot at a time, but it is capable of motion surprisingly rapid for a salamander; it then aids the action of the legs by a sinuous movement of the whole body. The tail is prehensile. When caught and touched, the salamander will sometimes strike the tail forcibly against the surface on which it stands, accompanying this act with a quick motion of the hind limbs whereby the animal will jump a distance of four to six inches, rising two or three inches in doing so. Like its relative, *lugubris*, this species is, in captivity, given to climbing. Van Denburgh's (1895*b*, pp. 777, 778) account follows.

A large *Autodax iëcanus* and fifteen eggs were sent me from Los Gatos, July 23, 1895. The eggs were evidently those of a batrachian, doubtless of this species. Each egg was about 6 mm. in diameter, almost spherical, and inclosed in a thin, tough, gelatinous sheath. Each of these sheaths was drawn out, at one place, into a slender peduncle, which was attached to a basal mass of the same gelatinous substance. In this way, each egg was at the end of an individual stalk, and all were fastened to a common base. This base had evidently been anchored to a stone or lump of earth. The eggs were in the early stages of segmentation. The following note accompanied them: "The salamander and eggs were found under the platform in front of a barn, in dry earth next the foundation wall, and about fifteen inches or more below the surface. The ground had been filled in, and was full of spaces. There was some dry rotten wood near the eggs. One or two smaller salamanders were near. About twice as many eggs were found as sent. There was no water within ten or fifteen feet." The salamander sent with these eggs was a female, and had a very large number of minute eggs in its ovaries.

On July 30, 1895, I killed a very large Autodax which had been sent me, from Los Gatos, several days before. It contained twenty-five eggs exactly like those described above, except that they lacked the gelatinous covering. These eggs appeared to be still in the ovaries. There were twelve in the right side of the animal, and thirteen on the left. Besides these enlarged ones, there were many minute ova.

A female of this species of salamander and seven pedunculated eggs were taken at Laytonville, Mendocino County, on July 1, 1913. They were found 9 inches (228 millimeters) below the surface of the ground in a cellar. These eggs were deposited in a group and attached by their peduncles to the damp earth. Now (1924) they measure 5.9 to 6.4 millimeters in diameter, being slightly elongated in the direction of the peduncle. The peduncle is 0.5 to 1.0 millimeters in diameter and the length between the egg and the point of attachment

is about 5 millimeters. A young individual, about 50 millimeters in length (with tail broken) and probably of the previous season's brood, was collected at the same time, but whether in immediate association with the adult and eggs was not stated.

Aneides lugubris lugubris (Hallowell). Arboreal Salamander

(Pl. 9, fig. 20; text figs. G, N)

[?]*Triton tereticauda* Eschscholtz (1833, p. 14).

Salamandra lugubris Hallowell (1849, p. 126). Original description, type from Monterey, California.

Ambystoma punctulatum Gray (1850, p. 37). Type locality, Monterey.

Anaides lugubris, Girard (1858, pp. 8–10, pl. 1 [figs. 26–33]. General account.

Aneides lugubris, Hallowell (1859, p. 23, pl. 7 [no. 2, figs. 2*a*–2*c*]). Description and figure.

Anaides lugubris, Strauch (1870, p. 74). Monograph.

Anaides lugubris, Boulenger (1882*b*, pp. 52–53), part. Description.

Anaides lugubris, Yarrow (1883, pp. 22, 158), part. Locality records.

Autodax lugubris, Cope (1889, pp. 183–185, pls. 27 [figs. 1–4], 35 [fig. 3], 48 [fig. 15], text fig. 44), part. General account.

Aneides lugubris, Wilder (1896, p. 191). Lungless condition.

Autodax, Ritter (1899, pp. 311–312).

Autodax lugubris, Ritter and Miller (1899, pp. 691–704, 7 text figs.). Life-history.

Autodax lugubris, Ritter (1903, pp. 883–886). Life-history.

Autodax lugubris, Whipple (1906*b*, p. 1). Naso-labial groove.

Autodax lugubris, Miller (1906, pp. 741–742). Locality records.

Autodax lugubris, Hilton (1909, pp. 53–54). Locality records.

Aneides lugubris, Snook and Long (1914, pp. 511–528, pls. 25, 26). Cytological study of maturation.

Autodax lugubris, Ruthling (1915, p. 62). In Santa Monica Mountains.

Autodax lugubris, Fowler and Dunn (1917, pp. 12 *et. seq.*, 23). Locality records; evolution.

Aneides lugubris lugubris, Grinnell and Camp (1917, p. 134, fig. 2). Range.

Aneides lugubris lugubris, Stejneger and Barbour (1917, p. 21; 1923, p. 18). Range.

Aneides lugubris, Stephens (1921, p. 59). In San Diego County.

Aneides lugubris lugubris, Grinnell and Storer (1924, p. 653). In Yosemite region.

Diagnosis.—Size moderate among California salamanders, total length up to 162 millimeters (6⅜ inches); naso-labial groove developed; maxillary and mandibular teeth dagger-like, conspicuous, extending beyond commissure of jaws; temporal muscles swollen; costal folds 12; inner digit on each foot small, but not rudimentary; tail somewhat swollen at middle, but not distinctly compressed; body coloration dark reddish brown with scattered small dots (1 mm. or less) of pale yellow.

Comparisons.—Distinguished from other California salamanders except Plethodontidae by presence of naso-labial groove; from *Batrachoseps* by larger size, stouter body, greater development of

limbs, and smaller number of costal folds; from *Plethodon elongatus* by stouter form, larger maxillary teeth, 12 instead of 15 costal folds, and spotted instead of striped pattern of coloration; from *Ensatina eschscholtzii* and *E. croceater* by swollen temporal muscles, larger maxillary teeth, and 12 instead of 10 costal folds; from *Aneides ferreus* by greater development of inner digit on all feet, by stouter form, and by pattern of marking consisting of fine dots instead of 'marbling' of light color; from *Aneides flavipunctatus* by larger adult size, rounded instead of compressed tail, and dark red instead of black coloration; from *Aneides l. farallonensis* by larger adult size, stouter form, enlarged instead of tapered tail, and lesser number of light spots on body.

Description.—Form stout among the Plethodontidae, head large, limbs moderate; head wedge-shaped in outline from above, sides tapering to near the rounded tip; temporal region swollen and bulging both laterally and dorsally; muzzle flat-topped, thin in profile and rounded at tip; lower jaw overhung by muzzle; external nares terminal, separation equaling interorbital width; no canthus rostralis; length of muzzle slightly greater than that of orbit; orbit small, directed laterally; width of interorbital space half to two-thirds length of orbit; swollen temporal region reaching forward to middle of interorbital space, divided anteriorly by a median furrow, bulging laterally behind orbit; outline of upper lip sinuous, with a small lobe below orbit, commissure bent dorsally at posterior end; outline of lower jaw from below trapezoidal; chin slightly convex; gular fold conspicuous, continued up side of neck nearly to dorsal surface in some individuals; free portion of upper arm shorter than forearm; palm short, smooth; digits moderate, blunt-ended, slightly dilated at tips, in order of decreasing length 3, 4, 2, 1, innermost short; body cylindric, slightly swollen at midlength; costal folds 12, distinct; hind limb slightly larger than fore limb; free portion of femur nearly equal to tibia; sole smooth, as broad as long; toes longer than fingers, blunt-ended and slightly enlarged at tips, in order of decreasing length, 3, 4, 2, 5, 1 or 3, 4, 5, 2, 1; anal region not swollen; tail cylindric or oval at base, but not strongly compressed, bluntly tapered to end.

Tongue thin, moderate in size, filling half to two-thirds of width of mouth, attached along midline; internal nares small, placed well back from tip of muzzle and in from margin of jaw; vomerine teeth in V-shaped arrangement interrupted medially, between and behind internal nares; parasphenoid teeth in posterior part of mouth in narrow belt, widened and slightly divided posteriorly; maxillary and mandibular teeth large, lance-shaped, very pointed, with broad surface parallel to jaw.

Surfaces everywhere smooth.

General coloration (in life), upper surfaces of head, body and tail, and exposed surfaces of limbs, uniform dark red, paling slightly on sides where marked with varying numbers of spots 1 mm. or less in diameter of yellow; ventral surface pale yellow; in alcohol upper surface takes on a bluish cast, undersurface becomes dingy yellow. Young individuals (in life) nearly black, with diffuse-margined pigment cells of silvery tone on upper surface, and fine dots of white on undersurface.

MEASUREMENTS OF ADULT SPECIMENS OF *Aneides lugubris lugubris* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
2371	♀	Moraga Valley, Contra Costa Co....	Feb. 22, 1910	134	57	19.5	14.2	4.5	2.8	18.7	7.8	40	20.3	10.0
8252	♀	Berkeley, Alameda Co....	Feb. 10, 1904	144	63	23.8	15.0	4.4	4.0	20.4	7.3	41	24.0	11.7
5679	♀	3 mi. ne. Coulterville, Mariposa Co., 3200 ft...	June 3, 1915	150	64	23.8	15.7	4.5	3.6	22.2	9.0	41	25.0	12.0
7366	♀	North Fork, Madera Co., 2750 ft....	Mar. 8, 1920	150	68	21.8	15.0	4.7	3.4	21.6	9.0	40	24.5	11 4
4497	♀	2 mi. sw. Napa, Napa Co...	Dec. 16, 1912	153	70	22.2	16.8	4.6	3.2	21.2	9 1	39	23.6	11.4
4504	♂	2 mi. sw. Napa, Napa Co..	Dec. 16, 1912	131	57	19.0	15 0	4.2	2 6	18.5	8.2	35	21.0	10.0
2372	♂?	Moraga Valley, Contra Costa Co....	Feb. 22, 1910	145	67	24.4	14.8	4 5	3.6	21.7	7.4	34	22.7	11.3
5680	?	3 mi. ne. Coulterville, Mariposa Co., 3200 ft.....	June 3, 1915	159	68	25.3	17.3	4.7	4.2	21.5	9 2	40	25 0	12.0
4498	♂?	2 mi. sw. Napa, Napa Co..	Dec. 16, 1912	159	69	21 1	16 5	3.6	3 0	20.8	8.4	39	24 0	10.7
4505	♂	2 mi. sw. Napa, Napa Co..	Dec. 13, 1912	162	76	21.7	12.4	4.8	2.4	20.3	9.8	44	23.0	10.0

MEASUREMENTS OF ADULT SPECIMENS OF *Aneides lugubris lugubris*, ALL FROM STONEWALL CREEK, 6.3 MILES NORTHWEST OF SOLEDAD, MONTEREY COUNTY, CALIFORNIA, COLLECTED JULY 23 AND 25, 1919.

M.V.Z. No.	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
7224	131	55	21.2	13.8	4.0	3.4	19.8	9.0	35	22.4	9.7
7220	134	58	21.2	14.5	4.4	4.0	21.2	8.7	37	17.7	8.0
7213	137	60	19.3	12.6	3.8	3.5	19.1	8.0	37	20.0	9.7
7214	138	61	20.7	14.0	4.2	3.7	20.4	7.8	36	22.7	12.3
7215	142	63	21.5	16.2	4.2	4.2	21.7	9.4	38	25.7	10.0
7217	142	62	20.2	15.3	4.1	3.5	20.7	9.0	39	23.0	10.0
7212	142	67	21.7	14.2	3.6	3.8	19.3	7.6	35	21.2	9.2
7211	147	66	21.8	15.2	4.0	4.5	19.8	8.0	39	24.7	11.2
7216	150	66	22.3	16 2	4.4	3.7	22.3	9.2	41	24.8	10.3
7209	156	67	24.0	17.0	4.1	4.5	21.4	8.5	41	25.2	13.6

History.—This salamander first came to attention in 1849 when a specimen from Monterey was described by Hallowell as *Salamandra lugubris.* The following year Gray described a specimen from the same locality as *Ambystoma punctulatum.*

On page 14 of the fifth part of Eschscholtz' Zoologischer Atlas a species of salamander is described in the following words:

TRITON TERETICAUDA

In seinem Tagebuch führte Eschscholtz noch eine vierte Art von geschwänzten Batrachiern auf und beschrieb sie in seinem Entwürfen zu diesem fünften Hefte des Atlasses folgendermassen.

'*Triton tereticauda, laevis, rufo-ferruginea, ventre albo punctata, cauda acuminata, tereti.*

'Ist ähnlich dem *Tr. cristatus,* lebt in Californien, wo man das Thier bei der russischen Niederlassung Ross im November häufig unter Steinen antraf.

'Länge des ganzen Thieres 6 Zoll und auch mehr.

'Die Haut am ganzen Körper ebenfalls glatt, rothbraun, am Bauche mit einzelnen bläulich weissen Punkten bezeichnet. Der Schwanz fast von der Länge des Leibes, ziemlich fein, zugespitzt und walzenförmig. Die Beine und Zehen ganz wie bei *Tr. cristatus* beschaffen.'

Leider fand ich von dieser Art unter den von Eschscholtz mitgebrachten Thieren kein einziges Exemplar mehr vor, weshalb ich darüber auch Nichts weiter, als nur die Vermuthung angeben kann, dass dieses Amphibium, weil es dem oben Angeführten zu Folge einem runden [walzenförmigen] Schwanz haben soll, eigentlich wohl nicht zu den Tritonen, sondern zu den Salamandern gehört. (Rathke *in* Eschscholtz, part 5, 1833, p. 14).

The name *tereticauda* has been doubtfully considered to be a synonym of *T. torosus* (Grinnell and Camp, 1917). Cope seems not to have listed the name in his 1889 monograph. The remark "häufig unter Steinen antraf," in combination with the characterization "Haut am ganzen Körper ebenfalls glatt," could not apply to *T. torosus.* When on land, hiding in shelter under stones, *T. torosus* is rough-skinned. Unfortunately, no specimen of *"Triton tereticauda"* reached Rathke's hands, so we have no means of knowing definitely what species was involved. Rathke's remark on the allocation of the form indicates that he did not consider it related to his *Triton torosus.* The total length "6 Zoll und auch mehr" suggests *Aneides lugubris lugubris* rather than *Ensatina eschscholtzii* so I list it under the former, but as of indeterminable status.

Range.—*Aneides lugubris lugubris* is restricted to the central and southern portions of California. At the south it has been taken in San Diego County in the Sequoia Mine and on Sorrento Mountain near La Jolla (Stephens, 1921, p. 59). Orcutt (1885, p. 5) has listed

a salamander under this name from The Falls of the San Diego River and Stephens repeats this record; Grinnell and Camp (1917, p. 131, fig. 1) on the other hand refer the record to *Notophthalmus* [= *Triturus*] *torosus*. *Lugubris* has been recorded from "Coronado Islands," Lower California, on the basis of two specimens obtained February 22, 1908 (Van Denburgh and Slevin, 1914, p. 139). In southern California *lugubris* has been found at Los Angeles (Miller, 1906, pp. 741–742), along the base of the San Gabriel Mountains at Pasadena and Sierra Madre (specimens in Mus. Vert. Zoöl.), in the hills north of Claremont (Hilton, 1909, pp. 53–54), and in the Santa Monica Mountains (Ruthling, 1915, p. 62). Specimens from 3 miles southeast of Lankershim and from 3 miles south of Nordhoff, Ventura County, are in the Museum of Vertebrate Zoology. Cope (1889, p. 185) lists a specimen from Fort Tejon, collected by H. W. Henshaw.

In the central Sierra Nevada it has been taken in Madera County at North Fork, 2750 feet altitude (Mus. Vert. Zool.), and in Mariposa County, 3 miles east of Coulterville at 3100 feet (Grinnell and Camp, 1917, p. 134).

In the Coast Ranges it has been taken east to 22 miles southwest of Los Baños, Merced County (specimen in Mus. Vert. Zool.), but not at that town (compare Grinnell and Camp, 1917, *loc. cit.*). It is common in western Alameda County about Oakland and Berkeley, and north, interiorly, to near Napa, Napa County (Mus. Vert. Zool.). The northwesternmost stations of capture are Mendocino City (Grinnell and Camp, *loc. cit.*), Comptche and Willits, Mendocino County (specimens in Calif. Acad. Sci.). No specimens are at hand from the triangular area between the Los Baños record, central Monterey County, and Santa Barbara (where recorded by Fowler and Dunn, 1917, p. 23), but I believe that this is due to lack of collecting in that area at the appropriate season; for example, the country around Santa Margarita would seem to be suitable for the occurrence of the species. The record by Baird (1859*b*, p. 13) for "Columbia River" is undoubtedly an error.

Life-history.—*Aneides lugubris* is a common species in the vicinity of San Francisco Bay and in the coast redwood belt in Marin, Sonoma, and southern Mendocino counties. Elsewhere in its range it is evidently less numerous and ordinarily specimens are found only by diligent search or by chance, chiefly during the rainy season.

Aneides is unique among the salamanders of California if not in the whole Order Caudata in its ability and propensity for climbing

trees. This habit was first announced by Ritter in 1903 in connection with observations on the breeding habits of the species, and it has since been observed by other naturalists. Studies by Ritter (1903) and L. H. Miller (MS) were made on the *Aneides* population on the University of California campus at Berkeley. Miller had been engaged for some time in searching for *Aneides* and finally, in 1898, discovered a female with eggs on the ground (see Ritter and Miller, 1899). Industrious search in August and September of habitats known to be occupied by the species during the winter rainy period failed to yield additional specimens or eggs. In the summer of 1903 workmen were engaged in cleaning out cavities in the large live oaks (*Quercus agrifolia*) on the University campus preparatory to filling the openings with cement, and during the progress of this work more than one hundred adult *Aneides* and at least twelve bunches of eggs were discovered. This material formed the basis of a brief paper by Ritter (1903) and a longer manuscript by Miller recently placed in my hands, excerpts from which are quoted in order to fill out the present account.

I have found the species aboveground only once, when two individuals of small size (approximately 42 and 70 millimeters in total length) were discovered under bark on an oak stub at a height of about 4 feet (1.25 meters) aboveground.

Aneides lives both on the ground and in trees. Practically all of the specimens in collections save those taken by Ritter and Miller have been found on the ground. The animals take shelter under stones, or boards which have lain on the ground for some time, in rotted stumps and logs, and at least two have been taken in nests of the brown-footed wood rat (*Neotoma fuscipes*). The salamanders are to be found in these habitats during the daytime, from the beginning of the rainy period (late September or early October) until about May. During the midsummer months, as indicated above, they disappear. Whether the animals ascend the trees only during the breeding season is unknown. The arboreal retreats need to be investigated during the winter rainy period in order to determine this point. Neither young nor adults are to be found on the ground during the summer dry period, and many individuals (35 in one instance: Miller, MS) were found to occupy single cavities aboveground. One group was found at a height of 30 feet above the ground. Miller (MS) says that these salamanders are great travelers. There is the possibility that the terrestrial stock of *Aneides* simply retires to holes in the ground during

the summer dry period, as *Ensatina eschscholtzii* and *Batrachoseps attenuatus* are believed to do. That some of the individuals do remain on the ground is indicated by the three records given below of eggs found at the ground surface in the late summer or early autumn months.

Individuals of *Aneides lugubris* are sometimes found during the daytime in seclusion under rocks on dryish hillsides at long distances from trees or leafy débris of any sort. In Claremont Cañon near Berkeley several individuals were collected in different years under rocks on a certain south-facing grass-covered slope where the nearest trees were 100 yards or more distant. The soil on this hillside is, in late summer, hard and dry. It may be that some of the individuals of this species regularly resort to such shelters, venturing forth after dark when the temperature has fallen and the relative humidity of the atmosphere has in consequence been materially increased.

Certain peculiarities of structure and habit in *Aneides* seem to be adaptations toward arboreal life. The tail is somewhat prehensile (Ritter and Miller). Captive individuals on the edge of a table have been seen to use the tail in a precautionary way to insure against falling. Likewise captives may sometimes be made to suspend themselves by their tails after the manner of an opossum. The tail in the terrestrial *Batrachoseps* and *Ensatina* is easily fractured whereas this never happens with *Aneides*. The tail is believed to subserve a different function in those species, and in a critical situation such as attack by an enemy may be more useful *off* the animal in distracting the attention of the predator from the salamander itself. With *Aneides* the tail seems to be of prime service to the animal itself and there would therefore be little advantage in being able to sluff it. Resting specimens of *Aneides* often curl the tail in a lateral spiral; no other salamander (with the possible exception of *Ensatina*) is known to do this. This habit would seem to indicate a greater voluntary control of the tail muscles than is possible in other species, thus facilitating prehension.

In *Aneides* the tips of the digits are slightly dilated and at least in preserved specimens slightly concave beneath, a condition suggesting the expanded tips of the fingers and toes in the Hylidae, which are noted for their climbing ability. Miller (MS) notes that juvenile *Aneides* are better able to climb on the smooth surface of glass than are the adults.

The maxillary and mandibular teeth in *Aneides* are larger relatively than in any of the other amphibians of California. The teeth are dagger shaped, completely covered with enamel, and placed with the flat surface parallel to the outside of the jaw. When the mouth is closed they project beyond the line of meeting of the jaws. A practical way for a novice to distinguish between *Aneides* and *Ensatina* is to rub a finger over the end of the closed mouth, when the teeth of the former can easily be felt, whereas those of the latter can be detected only when the jaws are separated. It is evident that these large teeth serve some useful purpose in the economy of the species. Cope in 1869 (p. 109) when describing the related species *ferreus*, said: "This curious genus is furnished with by far the most powerful dentition of any existing Salamander, and resembles in this respect the genera of the coal measures, Brachydectes, Hylerpeton, and Hylonomus." Later (1889, p. 185) he says: "I have little doubt that it is more capable of inflicting a bite than any other of the American Urodela." This surmise was confirmed in 1919 when Mr. Halstead G. White, while collecting in the Santa Lucia Mountains for the Museum of Vertebrate Zoology, was bitten on the finger by one of these salamanders which was being taken from its hiding place in a rotted log. Ritter (1903) says it was reported that the adult animals collected from the trees at Berkeley "showed fight" and would seize a stick or finger thrust near them. A student reported the same reaction by an individual on the ground. Of six adults, associated in pairs with egg clusters, five proved upon dissection to be females and one a male; the male did not show fight, the females did.

A further possible use of the enlarged labial teeth is indicated by Miller (MS) who states that pieces of a fungus which grows in the tree cavities inhabited by *Aneides* have been found in the droppings of the animals; some of these were as much as 3 to 4.5 millimeters in length. Possibly this source of supply is resorted to when insect material is scant. It seems unlikely that insect life in sufficient amount could be found in the several cavities of an oak tree to support the large number of salamanders found tenanting certain individual cavities. The fungus may therefore be a reserve food supply. This point, however, is discussed later.

Aneides seems to have become so specialized in its terrestrial existence that it is no longer able to take up life in the water, although some of the species of Plethodontidae in eastern North America are able to live in water as well as on land. Miller (MS) confined an

adult *Aneides* in an aquarium containing well-aerated water but where the animal could not reach the surface. It lived about 53 hours, gradually becoming exhausted. A terrestrial example of *Triturus torosus* subjected to similar conditions lived for more than six days without visible signs of discomfort, although it perished after sixteen days of confinement. The embryonic *Aneides* seems better able to survive in an aquatic environment, as an embryo shelled out of its capsule on September 12 (1903) lived in the water until September 28, and another lived for thirty days under similar circumstances (Miller, MS).

An adult *Aneides* dropped into water usually struggles violently to regain the surface, but its movements are more like those of a lizard than of an aquatic salamander. Miller (MS) noted that specimens treated in this manner suspended the rapid pharyngeal respiratory movements seen in the animals when on land, and there was no movement of particles in the water which might suggest the presence of a respiratory current. In the case of one *Aneides* dropped into water, bubbles of air appeared at once on the sides of the body, and with another, similar bubbles appeared after being immersed for some seconds. This phenomenon suggests cutaneous respiration. The former animal was kept in the water for 60 minutes and the pinkish coloration of the body became slightly blue, suggesting imperfect oxygenation of the blood.

This salamander is strictly nocturnal in its activities. I have never seen an individual away from cover during the daylight hours. Captive specimens in terraria spend the day hidden under any available shelter, and come forth only after complete darkness; they are then quite active. The iris is black in this species while in *Triturus torosus*, which is active to some extent in the daytime, the iris is yellow. Miller (MS) visited a tree cavity known to be inhabited by *Aneides* at Berkeley an hour after full darkness had set in; the animals were still in the cavity though near the entrance. Only once have I come upon the animal at night. About the first of November, 1921, one was picked up as it walked across a sidewalk in Berkeley at about 11 P.M. The animal was at a distance of several feet from the nearest suitable cover, and hence was probably out foraging.

This species exhibits a strong negative phototropism and positive thigmotaxis. Upon throwing the rays from a lamp into a terrarium where specimens of *Aneides* are crawling about at night the animals retire quickly into any sort of shelter available. An individual placed

out in the middle of a well lighted room will immediately go toward the darker side or toward any dark object. Miller (MS) held a dark coat near the floor of a room where one of the salamanders was being experimented upon. The animal went directly toward the coat and when three inches away raised its head and looked at the coat; continuing it climbed up into the folds of the garment. Others responded in similar manner. As soon as a salamander was placed in contact with the side of a small hole, in wood or even in glass, it moved rapidly into the cavity, suggesting a strong response to contact regardless of other factors (Miller, MS).

Aneides lugubris, like the other members of the Plethodontidae, is both lungless and gill-less after leaving the egg. Respiration is believed to be carried on through the skin, through the vibratory movements of the floor of the pharynx, and through enlarged blood sinuses in the digits (see Ritter and Miller, 1899, fig. 3). With such dependence upon cutaneous respiration it is obvious that death would quickly follow daytime exposure in the dry climate of the California foothill country. Captive individuals which have escaped from the moist terarria in which they have been confined in rooms at Berkeley, usually perish on the first night of escape; if they do not, they invariably show considerable shrinkage in size and bodily configuration, indicating that they are ill suited to continuance in even a moderately dry atmosphere.

On rare occasions *Aneides* has been heard to utter a mouse-like squeaking note. Miller (MS) records two instances of this sort, once in the wild and once when a captive individual was being stimulated with an electric current in the laboratory. I have heard it on at least one occasion. How this salamander, without lungs or a vocal pouch, produces its note is unknown.

This salamander breeds during the summer months, egg deposition taking place in July and August and possibly in late June. The first eggs were discovered about July 24 (1898) on the campus at Berkeley when a group of 19 was found in dry soil at the base of a palm 50 meters from the nearest creek. Development was already advanced when the eggs were found (Ritter and Miller, 1899, pp. 697–700). In the summer of 1903, 12 egg clusters, of 12 to 18 each, were taken from cavities in live oaks on the campus (Ritter, 1903). Five eggs, apparently of this species, were found by C. L. Camp beneath stones in a rock quarry near Napa, Napa County, on September 1, 1916. Two lots of eggs numbering 17 and 16, respectively, were dis-

covered by Mr. Halstead G. White in hollow logs on Stonewall Creek, 6$\frac{3}{10}$ miles southwest of Soledad, Monterey County, on July 23 and 24, 1919. On July 14, 1920, Dr. V. E. Emmel took a lot of 14 eggs from beneath a flower box in the Botanical Garden on the campus at Berkeley.

The detailed record of the 1903 material, at Berkeley, in Miller's MS notes is as follows:

July 7 or 8	Four or five adults in cracks and crevices in a hole in a tree.
July 15 (about)	Three *Aneides* about two years old in nest 6 feet above ground; animals up in cone-like apex of hole.
July 22	Eight and 12 animals, respectively, of all sizes, in two holes in a California buckeye; second hole closed at entrance save for small irregular opening which appeared like a mere surface abrasion.
July 28	Four salamanders in hole 14 feet aboveground.
August 6	Two large *Aneides* and 3 eggs in hole at least 16 feet aboveground; one adult resisted removal and snapped viciously when caught by the tail. Cavity small and open, animals covered with moss, and eggs suspended from top of cavity.
August 7	''Nest,'' not investigated, 6 or 7 feet aboveground; 4 or 5 eggs suspended from 'ceiling' and a large animal seemed to be coiled about them.
August 15 (about)	An adult coiled about her eggs.
August 18 (about)	Set of 13 eggs, with embryos well advanced in development squirming about in their capsules.
August 24	Set of 10 eggs, embryos younger, still unpigmented, and not moving.
August 29	Two adult females and 14 eggs taken in hole at least 30 feet aboveground; orifice not more than one inch in diameter.
September 7	Two adults and a 'batch' of eggs well advanced in development.
September 10	Four batches of eggs, one cluster of 14 well advanced in development, two of 12 and one of 16, the last taken from oak next to LeConte Oak, with two large adults and three 'yearlings' in hole 20 feet aboveground.
September 17	Two adult females and 7 eggs far advanced in development; three eggs hatched this date though prematurely. Females contained white ''ovules'' about 2 mm. in diameter and few in number, forming a row ''the length of the abdominal cavity.''
September 19	Thirty-five salamanders and bunch of 14 eggs (attended by adult male and female), all from one hole. Eggs in early stages of development. Female contained large ova as in previous specimens.

The eggs, as already described by Ritter and Miller (1899), are separate, not in masses like the eggs of the water-spawning Caudata. Each egg is attached by a single slender twisted peduncle to the 'roof' of the nest chamber and the end of each peduncle is 'plastered' against the superstratum. This basal material can be teased out into a long string of material like that composing the peduncles and egg capsules; one of these strings was 100 millimeters long, and fragments aggregated 50 millimeters more. There is no scar on the opposite side of the eggs as described by Snyder for *Batrachoseps*. The stalks of the several eggs are twisted about one another giving a braided appearance to the base of the whole mass. The peduncle is 8 to 20 millimeters in length and about 1 to 2 millimeters in diameter. The eggs externally measure from 6 by 7 millimeters to 9.5 millimeters in outside diameter, the former being slightly oval, the latter more rounded and advanced in development (Miller, MS). The material from Monterey County measures about 6 millimeters in outside diameter.

As indicated in the notes on the 1903 material, an adult animal (female) is usually in attendance upon the eggs. Suspension of the eggs from the roof of the cavity permits the salamander to bring its body closely in touch with the eggs. Parental attention seems to be necessary for at least two reasons. Eggs left to themselves usually perish through desiccation; the parent individual therefore provides moisture, either from her skin or from the bladder, which in the case of adults in attendance upon eggs is usually found to be distended with fluid. Adult individuals in attendance upon eggs brought into the laboratory have occasionally been found to devour their own eggs. Whether this happens in the wild or whether other adults attempt to prey upon the eggs (as males of *Triturus torosus* are known at times to do with eggs of that species) is unknown. Should attempts of this sort occur in the case of *Aneides* the sharp teeth of the guarding female would appear to be an effective protection against such attack.

The 'embryonic' and 'larval' stages of this salamander are both passed within the egg capsule. Gills are developed and these spread out and perform a function analogous to that of vitelline vessels in the higher vertebrates. The gills disappear before birth and the young salamander at birth is in general like the adult. No lateral line organs are developed, nor is a tail fin in evidence at any stage. However, not all of the yolk material is consumed before hatching, so that the recently emerged *Aneides* carries with it a small store of nutriment.

The chronology of development in the material secured by Dr. Emmel in 1920 was as follows:

July 14, eggs found; anterior limb buds well developed, but posterior ones not clearly defined; no gills.
July 20, gills developing.
July 23, gills expanding posteriorly, rather thick, sac-like vessels with main loop developing a capillary network.
July 26–31, gills all expanded.
August 29, one larva began to hatch but died in the attempt.

The material found in 1898 hatched on September 13, about 50 days after being found, and, as the eggs had already commenced to develop when discovered, an incubation period of approximately two months is indicated. One individual at hatching was 32 millimeters in total length. The first young in the 1903 material hatched out on September 11; it was then 26.5 millimeters long. Several young which hatched from a cluster on September 15 showed great activity in climbing as soon as they came into contact with wood; individuals would cling to a stick by coiling the tail about it with the aid of one hind foot. Ritter (1903) suggests that the young born in the oak tree cavities at Berkeley may have remained aboveground for the first year of life. Young, in cavities of any sort, tend to group together, presumably to avoid desiccation. A few individuals of small size are to be found on the ground, but a majority of those discovered in terrestrial retreats are of larger size. Dispersal of the young probably occurs after the autumn rains.

Several specimens in the collection of the Museum of Vertebrate Zoology contain well developed ovarian eggs. No. 8252, collected in North Berkeley, February 10, 1904, and kept alive until February 23, contains 27 ova, the largest 4 millimeters in diameter; nos. 8253–55, taken in Sutro Forest, San Francisco, February 15, 1912, contain eggs up to 4 millimeters in diameter; and no. 5679, found 3 miles east of Coulterville, Mariposa County, on June 3, 1915, contains eggs up to 4.3 millimeters in diameter. The latter would probably have soon been laid.

On one occasion a recently hatched specimen of *Aneides lugubris* was found in the water coming from a drinking fountain on the University of California campus. This specimen, 28 millimeters in length, was obtained in October, 1913.

A series of 36 well preserved specimens of *Aneides* collected 2 miles southwest of Napa, Napa County, on December 13 and 16, 1912, affords an opportunity to study the growth of this species subsequent

to hatching. These specimens range from 32 to 162 millimeters in total length. Grouping these by differences of 10 millimeters in total length the following results are obtained:

25–34 mm.	1	75– 84 mm.	3	125–134 mm.	4
35–44 mm.	5	85– 94 mm.	2	135–144 mm.	0
45–54 mm.	3	95–104 mm.	1	145–154 mm.	1
55–64 mm.	1	105–114 mm.	5	155–162 mm.	2
65–74 mm.	6	115–124 mm.	2		

The grouping here suggests that the animals of the season's brood range up to about 50 millimeters in total length; those of the next brood about 70 millimeters in length; of the third year about 110 millimeters long; of the fourth year 130 millimeters; and of the oldest group, 5 years or more of age, over 140 millimeters in length.

Aneides lugubris feeds upon insects to a considerable extent. Cope (1889, p. 185) states that in the stomach of one specimen he found ants, in another three or four species of beetles including an entire Coccinellid. The present writer has found insect fragments in the stomachs of museum specimens. The female with well developed eggs collected February 10, 1904, contained a *Batrachoseps* when it was killed 13 days later; this may have been obtained in captivity as the specimen was only partially digested.

Two adult *Aneides,* male and female, captured with a set of eggs on September 19, 1903, had, by September 24, passed a number of pellets of faeces and these were examined carefully as to contents.

> They showed hard parts of insects, legs, wing covers, etc., numbers of amoeboid bodies, spores of fungi and *chips of wood.* I had previously suspected the animal of eating the softened wood and fungus. The richness and abundance of the damp fungus would make it an easy food. The presence of oak fibers in a number of faecal pellets and abundance of fungus spores possibly gives the dark color to the stomach contents and the faeces. One piece of wood was 3 mm. in length and another 4 mm. The mass of the faeces is made up of wood fiber, spores and spore masses. . . . A mass of wood fibre and fungus was brought in from the tree where so many salamanders were found together and examined for insect forms. Three or four small spiders and a couple of . . . insects were all that could be found. The amount of such life in a cavity that is so thoroughly peopled as the one last seen would be entirely insignificant as a food supply for the whole colony. The fungus spores and wood fibers are identical with those taken from the faeces. (Miller, MS.)

The life-history in relation to the environment.—*Aneides lugubris* appears to be the most specialized of the salamanders occurring in California with respect to its adjustment to environmental conditions. It seems to have gone about as far as a non-aquatic salamander can

go in the direction of terrestrial existence, short of the development of a dermal armor to check loss of moisture. The three genera of Plethodont salamanders in central California seem to represent three distinct ecologic types, one (*Batrachoseps*) occupying small holes in the ground such as made by earthworms and other invertebrates, a second (*Ensatina*) living in terrestrial burrows of larger animals (Mammalia), and a third type (*Aneides*) dwelling at or above the ground surface in rotted logs or stumps, in wood-rat nests, and in rotted-out cavities in live oaks. Ecologic competition in the matter of daytime refuges and breeding places would seem to be avoided, and there seems to be some segregation with respect to food habits as well.

It seems not without significance that the range of *Aneides l. lugubris*, so far as known, does not extend far if at all beyond that of the California live oaks (*Quercus agrifolia* and *Q. wislizenii*). The arboreal shelter offered by the oaks at Berkeley (before they were cemented) would probably be duplicated in the trees of this group at other places within the State. The other local species of oaks may or may not afford conditions suitable for this salamander. The golden oak (*Quercus chrysolepis*) occupies a somewhat wider range than the species previously mentioned and might be serviceable to *Aneides*. Suitable cavities may occur, for example, in the valley oak (*Q. lobata*) of the Sacramento-San Joaquin basin and other interior valleys, but *Aneides* could scarcely be thought to live, or at least to spread, as a species, under present climatic conditions in the Great Valley where there are frequent winter floods and prolonged summer dry periods; the deciduous blue oak (*Q. douglasii*) of the foothills seldom affords cavities of a size suited to the requirements of a salamander; the black oak (*Q. kelloggii*) has smoother bark and is often of tall habit, involving greater danger of falling to an animal of imperfect scansorial development. Furthermore, the cavities in this species of oak are made use of by arboreal squirrels (*Sciurus griseus* and *Glaucomys sabrinus*) which fact might preclude their use by a salamander. If the observations by Miller (MS) indicating use of fungus as food, particularly during the summer season, represent a normal habit of the species, the possible restriction of this fungus to the live oaks might be a factor in controlling distribution.

Several structural specializations of *Aneides* point toward success in arboreal life. These are the prehensile character of the tail, short digits with expanded tips, development of blood sinuses in the

toes where likely to come into contact with the moist substratum either on the ground or in a cavity in a tree, and large size of maxillary and mandibular teeth placed *at the margin* of the jaws where most likely to be of service in offense or defense and where most serviceable in gnawing off fungus or enlarging the entrances to cavities in rotted wood. The jaw teeth of *Aneides* are different in form and placement from those of other Plethodonts or other amphibia generally, and their semi-exposed location parallels the unobstructed placing of the incisor teeth of rodents.

The period of egg deposition with *Aneides* coincides with the time of maximum summer heat and dryness and might be thought to indicate persistence of an ancestral summer-spawning period in the face of adverse climatic conditions. However, I believe a simpler and more logical explanation is possible. Since the adult (female) guards and probably supplies moisture to the eggs, the danger of desiccation is obviated. Emergence of the young at some time in the spring months, particularly if they happened to be born in a tree cavity, would leave ample opportunity for them to perish through desiccation. But with egg deposition in July or August, followed by a period of development lasting for about two months, the time of emergence of the young animals is at or after the advent of the first autumn rains. Thereafter the days are less hot, the ground retains its moisture more readily, young salamanders would be less likely to be killed by desiccation, and many species of insects would then be initiating their developmental cycle, affording stocks of larvae or soft bodied small-sized insects upon which the young salamanders might feed. Furthermore, dispersal from the parental tree cavity would be fraught with less danger during the rainy period than were it to occur at the beginning of the summer dry season.

Whipple (1906*a*) has advanced the argument that the lungs of salamanders are chiefly hydrostatic in function, basing her contention on the fact that the aquatic urodeles living in relatively quiet water, possess a pre-pubic ''ypsiloid'' cartilage, which is of service in compressing the abdomen and hence the lungs, whereas the terrestrial species (Plethodontidae) lack this structure. More recently Wilder and Dunn (1920) have put forward the theory that the Plethodontidae originally were inhabitants of mountain brooks, and that the loss of lungs was due to lack of need for these organs in the habitat mentioned. The Appalachian Mountain region, which for a long geological period is believed to have afforded this habitat, is indicated

as a center of development for the Plethodont stock. If these suppositions are correct, and the arguments and data advanced seem in some degree to uphold the views mentioned, then our strictly terrestrial (or non-aquatic) western Plethodonts are to be thought of as stock which has completely left the water and is able to live successfully on land despite the loss of lungs which might be thought to be of more service in respiration in a terrestrial environment.

According to Dunn (1923*a*, p. 39) one species of Plethodont from eastern North America, *Plethodon aeneus* Cope and Packard, of the Cumberland Mountains in West Virginia and Tennessee, is congeneric with *Aneides lugubris.* This disposition, if correct, indicates a considerable degree of antiquity for the *Aneides* stock, as conditions in the territory between the present ranges of the eastern and western species have apparently been unsuited for the migration of land salamanders for a large part of Tertiary time.

Aneides lugubris farallonensis (Van Denburgh)

Farallon Salamander

Anaides lugubris, Boulenger (1882*b*, pp. 52–53), part. On Farallon Islands.

Anaides lugubris, Yarrow (1883, pp. 22, 158), part.

Autodax lugubris, Cope (1889, pp. 183–185), part.

Autodax lugubris, Keeler, *in* Blankenship and Keeler (1892, pp. 151, 154). Status.

Autodax lugubris farallonensis Van Denburgh (1905, pp. 5–6, 28, pl. 2). Original description, type from South Farallon Island, California.

Autodax lugubris farallonensis, Van Denburgh and Slevin (1914, p. 134). Occurrence.

Aneides lugubris farallonensis, Grinnell and Camp (1917, p. 135, fig. 2). Range.

Aneides lugubris farallonensis, Stejneger and Barbour (1917, p. 21; 1923, p. 18). Range.

Diagnosis.—As for *Aneides lugubris lugubris* (which see), but temporal region of head less swollen, limbs, digits, and tail more slender, and spots on body more numerous.

Comparisons.—See *Aneides lugubris lugubris.*

Coloration.—General body color above near Hay's brown, darkest on middle of back, paling on sides of body and tail; upper surface and sides of body and exposed surfaces of both fore and hind limbs profusely marked with spots of colonial buff, these varying from mere pin-points to spots 1.5 mm. in diameter; legs and lower sides of head, near vinaceous buff, varying in tone; tips of digits usually bright red, due to concentration of blood in sinuses (color description from living specimens collected September 6, 1922).

MEASUREMENTS OF ADULT SPECIMENS OF *Aneides lugubris farallonensis* FROM SOUTH FARALLON ISLAND, CALIFORNIA

M. V. Z. No.	Date	Total length	Length of tail	Snout to gular fold	Greatest width of head	Orbit	Interorbital space	Fore leg	Hand	Axilla to groin	Hind leg	Hind foot
8588	Sept. 6, 1922	126	54	19.0	13 6	4.0	3.0	18.8	9.1	35	22.7	12.0
8600	Oct. 26, 1922	126	54	18.2	13.5	3.6	2.5	20.4	8.6	33	22.0	11.4
8601	Oct. 26, 1922	130	60	16.5	12.5	3.5	2.6	17.6	7.0	36	19.4	10.2

History.—Early specimens of this form were included under the name of the mainland form. In 1905 Van Denburgh described the island form as distinct.

Range.—*Aneides lugubris farallonensis* is confined to South Farallon Island, which is in the Pacific Ocean about 28 miles west by south offshore from San Francisco.

Life-history.—The occurrence of a stock of *Aneides lugubris* on the Farallon Islands has been known at least since 1882 (Boulenger). One writer (Keeler, *in* Blankenship and Keeler, 1892, p. 151) has ventured the statement that the salamanders may have been introduced in recent times through the agency of man. For many years prior to 1900 the Farallon Islands were visited each summer at frequent intervals by men from San Francisco who collected eggs of the California Murres which nest on the island for the city markets. This traffic probably suggested to Keeler the possibility of the salamanders having been introduced. The introduction of trees, for example Monterey cypresses, carried as nursery stock to South Farallon, would have afforded a possible means of transport. But the fact that the island population of *Aneides* differs from the mainland stock in structure and coloration indicates that it has been present there over a long period of time, without doubt since the Farallones were last separated from the Coast Range.

On August 18, 1922, I visited South Farallon Island and during the afternoon made a search for *Aneides l. farallonensis.* The ground above the surf was everywhere quite dry and although I turned over many rocks and boards no specimens could be found. The animals were presumably in deeper shelter where adequate moisture was available. I was told that a short time previously several of the salaman-

ders had been found beneath a pile of boards near the east end of the island. The lighthouse attendants were well acquainted with the species, saying that the salamanders "came out at night." Mr. Fred Zimmermann of the station kindly consented to get some specimens for me and on September 6, 1922, I received two living examples from him. These formed the basis of the color description given above. In general behavior these animals were like examples of the mainland subspecies from Berkeley which have been handled in captivity. If anything, the island animals were even more active by daylight than the Berkeley *Aneides* under similar conditions.

On October 26, 1922, Dr. H. C. Bryant collected a series of eleven specimens of this salamander. These specimens (nos. 8588–99, Mus. Vert. Zool.) exhibit the annual growth of the subspecies fairly well. They range from 39 to 126 millimeters in total length. Three which measure 39 and 40 millimeters are undoubtedly of the 1922 brood (compare measurements of newly hatched *lugubris* at Berkeley). One with a blunt (regenerated?) tail, 53 millimeters in total length, and a normal individual 62 millimeters long, are taken to represent the 'yearling' class. Five others 101 to 112 millimeters in length are either three or four years of age and one is 126 millimeters and hence four or five years old.

There is a limited amount of insect life on South Farallon and this evidently suffices for the needs of the *Aneides*. At the present time shelter is afforded under piles of boards, and in the basements of buildings; under original conditions cavities under loose rocks and deserted burrows of sea birds were available. There have been no native trees on South Farallon in historic times and so the salamanders have of necessity been required to be terrestrial in habit. The smaller size of the tail in the island stock probably reflects lessened use of that member as compared with the tail in the mainland stock.

The Farallon Islands lie in a general line of continuation of the mountains of Monterey County, the exposed rocks on the islands resembling to some degree the rocks at the northwestern tip of Monterey County, and the sea terraces, as pointed out by Blankenship (*in* Blankenship and Keeler, 1892, p. 146), on South Farallon and at Carmel are at closely corresponding levels. It is possible that the islands represent a series of high peaks, in general continuation of the Santa Lucia Range, which have been all but submerged in the most recent subsidence of the Coast Range. Interest in the geological aspect of the Farallones is heightened by the discovery in 1919, by a

party from the Museum of Vertebrate Zoology, of a stock of *Aneides lugubris* in the mountains of Monterey County, which resemble in considerable degree the island form, *farallonensis*. These animals are much more heavily spotted than the mainland stock and the general form of the body is more like that of *farallonensis* than *lugubris*.

Ascaphus truei Stejneger. American Bell-toad

(Text figure KK)

Ascaphus truei Stejneger (1899, pp. 899–901, pl. 89, 4 text figs.). Original description, type from Humptulips, Chehalis County, Washington.

Ascaphus truei, Van Denburgh (1912*c*, pp. 259–264, 1 fig.). Habits in brief; external structure and osteology (based on Washington specimens).

Ascaphus truei, Grinnell and Camp (1917, p. 140). Occurrence in Siskiyou County, California.

Ascaphus truei, Stejneger and Barbour (1917, p. 25; 1923, p. 22). General range.

Ascaphus truei, Gaige (1920, pp. 1–10, pl. 1). Habits, eggs, larvae, and life-history in western Washington.

Diagnosis.—Size small, head-and-body length (exclusive of 'tail') up to 50 millimeters (2 inches); short tail-like process 6–8 mm. long, traversed by cloaca, present in males; pupil of eye vertically elliptical; tympanum absent; digits very slender; three tubercles in transverse row on palm; one (inner) metatarsal tubercle; outer (fifth) toe stoutest; surfaces everywhere exceedingly smooth; tongue disk-like, occupying whole floor of mouth, and broadly attached.

Comparisons.—Distinguished from all other California Salientia by absence of tympanic membrane, by presence of vertically elliptical pupil together with absence of cutting spade on hind foot, by presence of three palmar tubercles in transverse row, by very large size and rounded form of tongue, and, in males, by presence of tail-like process at end of body.

Description (based on specimens from Mason County, Washington).—General form depressed; muzzle obtusely pointed in outline from above, flat-topped and abruptly rounded at tip in profile; external nares about midway between tip of nose and orbit, very small, aperture nearly round; canthus rostralis distinct between naris and orbit; orbit moderate, pupil vertically elliptical; interorbital space flat, its width about two-thirds length of orbit; no tympanic membrane; parotoid glands low, imperfectly indicated, divergent posteriorly; lower jaw evenly rounded in outline; no vocal sac; gular fold small and incomplete; dorsal surface of body evenly rounded; fore limb slender; fully half of upper arm free from body skin; forearm about equal to hand in length; three conspicuous tubercles in transverse row on palm of hand, inner one largest; no subarticular tubercles; fingers slender, third longest, second and fourth equal, inner shortest; femur practically free from skin of body; tibia slightly

longer than femur; hind foot about three-fourths length of body; tarsus about two-fifths length of foot; one low inconspicuous metatarsal tubercle at base of innermost toe; toes slender except outermost, which is broad and flat; toes, in order of decreasing length, 4, 3, 5, 2, 1; webs very short, reaching about to end of innermost phalanx on fourth toe, but a narrow edging of web on side of each toe.

Tongue broad, practically filling mouth, closely margining lower jaw anteriorly, truncate behind, broadly attached for anterior two-thirds to floor of mouth; internal nares small, widely separated, well back from tip of nose, opposite anterior border of orbit; vomerine teeth in two small separate rounded patches between nares.

Surfaces of body everywhere smooth, with few low granular papillae on dorsal surface of body; plantar surfaces of palms and soles smooth.

General coloration (in alcohol) above, dark gray; triangular patch covering posterior half of each eyelid and posterior part of interorbital region, blackish; forepart of head above, pale gray; spot below nostril on each side of snout, stripe behind eye, bar on fore limb, and several rows of small spots on back, blackish; exposed surfaces of limbs specked with dusky; ventral surface of body light grayish anteriorly, yellowish posteriorly.

Gaige (1920, pp. 4–5) gives the following color descriptions of the living animals as seen in Washington.

> Female: back cacao brown, light spot on head pinkish cinnamon, warts on sides and legs cinnamon buff, sides of head and body dark olive buff, below flesh color which was most distinct on chin and legs, belly densely spotted with mustard yellow. A live male differed from the female in having a citrine drab back and the warts cacao brown; the "tail" above was the color of the body with a dark stripe down either side, beneath darker. The ground color is most commonly old rose or brick red, but it may vary from cream white, through various shades of pink, gray, and brown to almost black. In the lightest and darkest specimens the pattern is fairly well obscured. The glandular ridge or row of glandules on the side is usually dark tipped with golden yellow; the dark spot on the head is almost triangular; the dark line on the wrist is seldom interrupted; the upper surface of the limbs is often set off from the lower by a dark line which merges gradually into the color beneath. The females are usually more brightly colored than the males.

Description of larva.—Head-and-body 18 mm.; tail 22 mm.; body slightly wider than high; external naris protruding, nearer to orbit than tip of snout, aperture lateral; eyes small, well up on dorsal surface of head, interorbital space 3.5 mm.; spiraculum ventral, a transverse slit about midway of head-and-body length; anus median, concealed by a ventral flap of skin; tail fin moderate, dorsal part evidently originating close to upper base of tail; mouth region concave, 8 mm. wide, 7.5 mm. in opposite (anteroposterior) dimension; upper lip (beak) a nearly straight transverse band of black about 6 mm. long; lower lip minute, concealed beneath upper; labial teeth in $^{3}/_{10}$ rows, occupying entire width of mouth region, first 'row' multiple, of several rows of minute teeth, second and third rows double, fourth row (just below mouth) interrupted at midline, sometimes doubled,

remaining rows single and continuous across mouth region, individual teeth progressively smaller in lower rows; numerous minute rounded papillae on lower lip; a soft flap of skin at either side of mouth (fig. KK). Color in alcohol, brownish black with a bluish iridescence on body (based on 40 mm. larva, no. 8502, Mus. Vert. Zool.).

MEASUREMENTS OF ADULT SPECIMENS OF *Ascaphus truei* FROM STAIRCASE CAMP, MASON COUNTY, WASHINGTON, COLLECTED JULY 1, 1922

M. V. Z. No.	Sex	Head-and-body length	Tip of muzzle to angle of jaw	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
8496	♀?	40.5	13.1	15.8	5.8	4.2	10.8	10.5	17.6	20.5	13.5	28.5
8497	♂	41.0	13.0	14.3	7.5	4.0	10.0	9.5	16.4	20.0	12.0	28.5
8498	♂	41.4	12.8	14.7	6.0	3.8	10.0	10.2	17.3	19.8	12.8	29.2

History.—*Ascaphus truei* was described in 1899 on the basis of a specimen collected in western Washington by Cloudsley Rutter on August 19, 1897.

Range.—This distinctive amphibian has been found in a limited area on the northwestern coast of North America between the crest of the Cascade Mountains and the Pacific Ocean. In Washington it has been found in creeks near Lake Cushman, in Mason and Jefferson counties (Gaige, 1920, pp. 2–4), at Humptulips, Chehalis County (Stejneger, 1899, pp. 900–901), at North Bend, King County, altitude 2000 feet (Van Winkle, 1922, pp. 4–6), on Mount Rainier, Pierce County, near Reflection Lake, altitude about 4861 feet, and at Indian Henry's Hunting Ground, altitude about 6000 feet (Van Denburgh, 1912*c*, pp. 259–260). In Oregon it has been found on Red Creek in the Santiam National Forest, Linn County, altitude 3000 feet (Camp, 1917*a*, pp. 13–14). The southernmost locality of record and the only one to date for California is Craggy Peak, Siskiyou Mountains, Siskiyou County, 5000 feet altitude (Grinnell and Camp, 1917, p. 140).

Life-history.—The important points in the life-history of this remarkable amphibian have been ascertained by Mrs. Gaige (1920) who spent several weeks studying the species in creeks near Lake Cushman, Mason County, Washington. More than one hundred individuals were obtained in the course of this study. Practically all of the adult toads were found in flowing mountain streams where the water was of low temperature (usually under 40° F.) and where the

banks were heavily forested. Like *Rana boylii* in California, *Ascaphus* lives solitarily in the stream or no farther away than the adjacent shore. The adults take shelter under stones in the water and when these are lifted the toads either remain motionless on the bottom or else float passively downstream amid the débris. When removed from their native habitat the adults perish quickly unless kept in melting ice water or in a refrigerator. A very low thermal death point is indicated, probably the lowest for any amphibian living in the United States.

Two instances have been recorded of the finding of *Ascaphus* out on land away from streams. Van Winkle (1922, pp. 4–6) found three individuals among fallen timber and underbrush on a wooded mountain slope near North Bend, Washington; there had been a heavy rain the night before and the moss, brush, and trees were wet. In a note appended to the foregoing account G. K. N[oble]. gives the experience of Mr. Philips G. Putnam, who, following several days of rain, found four *Ascaphus* out on land, one of them over 100 feet from the stream. This particular toad had not begun to absorb the larval tail.

No mention is made by either Van Denburgh or Gaige of a vocal sac, nor is one to be seen on specimens at hand from Lake Cushman. Presumably the voice has degenerated, being of no value to a species so strictly aquatic as *Ascaphus*. Males of the European species of the Discoglossidae, which are of terrestrial habit, have voices like other Salientia. The reduction in voice of *Rana boylii* and *Rana draytonii* in California may be a parallel development to that in *Ascaphus*.

Breeding males, according to Gaige (1920, p. 5), have the forearm enlarged to two or three times the normal size, the inner palmar tubercle is similarly increased and where the latter touches the forearm a white horny patch is developed; several individuals had this patch, the inner side of the first two fingers, and the inner palmar tubercle, covered with black. The underside of the forearm becomes gray thickly dotted with white.

Gaige found females containing eggs and males showing the highly developed secondary sexual characters of the species from June 27 to "early September," which she interprets as meaning a prolonged breeding season. Eggs were found in a creek on August 5, and a full-grown tadpole was collected on June 25. This latter individual was 45 millimeters in total length. Although no dates or localities are given regarding tadpoles, one gets the impression from reading Gaige's account that they were found at various dates through the season.

Philips Putnam has sent two larvae to the Museum of Vertebrate Zoology (now no. 8502) collected on July 2, 1922, near Lake Cushman. These two differ greatly in size, measuring respectively, 26 and 40 millimeters in total length. The mouthparts of the smaller of these is shown in text figure KK. It seems, from the fragmentary data available, that *Ascaphus* probably spawns through a considerable period during the midsummer months and that the larvae do not metamorphose within a brief season as is the case with some of the land-dwelling Salientia. The size of the larger tadpole mentioned above and the date of capture suggest overwintering in the larval condition, as is practiced by *Rana boylii sierrae* in the Sierra Nevada of California.

A young *Ascaphus* from Triple Trip Creek, Mason County, collected July 12, 1922, is 22 millimeters in head-and-body length. Judging from the size attained by larvae, this specimen had probably metamorphosed only a short time before it was collected.

The life-history in relation to the environment.—Aside from the fact that it is the only member of the suborder Costata in the Western Hemisphere, *Ascaphus truei* is remarkable in that it presents what is probably the most extreme case of close adaptive specialization in relation to habitat of any of the Salientia of western North America. Its known geographic range includes only areas in the Canadian (and Transition?) Life-zone in the northwest coast region, where the streams are perennial, swift flowing, and of low temperature. In habits it differs markedly from the species of costate Salientia found in southwestern Europe, whose life-histories are well known. The larva is supplied with a special 'sucker' or holdfast which enables it to cling to rocks in the stream and thus avoid being carried to warmer waters in the lower altitudes. Removal from the stream habitat leads to the early death of larvae (Gaige, 1920, p. 6). The adults likewise require low temperatures for successful continuance. The conditions of life for this species are radically different from those for practically all of the other Salientia discussed in the present paper. *Ascaphus* evidently has to avoid even moderately high temperatures whereas most of our California amphibia seek to avoid desiccation and their temperature tolerance is relatively great.

Scaphiopus hammondii Baird. Western Spadefoot Toad
(Pl. 2, fig. 3; pl. 10, figs. 25–30; text figs. W, EE)

Scaphiopus hammondii Baird (1859*b*, p. 12, pl. 28 [figs. 2*a*–2*d*]). Original description, type from Fort Reading [= near Redding, Shasta County], California.

S[*caphiopus*]. *hammondii*, Cope (1863, pp. 53–54). Critical.

Scaphiopus Hammondii, Cooper (1868, p. 486). At San Diego.

Spea stagnalis, Yarrow and Henshaw (1878, p. 209). At Santa Barbara.

Spea hammondii, Cope (1883, pp. 15, 32). Range.

Spea hammondii, Yarrow (1883, pp. 24, 177, 193). Range.

Spea stagnalis, Yarrow (1883, pp. 25, 177, 193). Range.

Spea hammondii hammondii, Cope (1889, pp. 305, 306, pl. 49 [fig. 8], pl. 51 [fig. 18], pl. 68 [fig. 1], text fig. 77). General account.

Scaphiopus hammondii, Stejneger (1893, p. 222). At Olancha.

Scaphiopus hammondii, Dickerson (1906, pp. 59–60). General account.

Scaphiopus hammondii, Stejneger and Barbour (1917, p. 25; 1923, p. 23). General range.

Scaphiopus hammondii hammondii, Grinnell and Camp (1917, p. 140). Range in California.

Scaphiopus hammondii, Stephens (1921, p. 59). At San Diego.

Scaphiopus hammondii hammondii, Grinnell and Storer (1924, pp. 654–655). Habits at Mono Lake.

Diagnosis.—Pupil of eye vertically elliptical; palms and soles of feet smooth except for a sharp-edged cutting 'spade' on inner part of metatarsus, and a narrow tubercle on inner edge of metacarpus; body relatively smooth, with many small rounded tubercles but no large warts.

Comparisons.—Distinguished from all other California Salientia by combination of vertically elliptical pupil and sharp-edged cutting 'spade' on each hind foot, together with relatively smooth skin on dorsal surface of body.

Description.—Head short, thick in profile, outline from above bluntly oval; lower jaw overhung by muzzle; external nares at sides of nasal boss and directed dorsally; canthus rostralis scarcely indicated; eyes large and conspicuous, orbit longer than distance from tip of muzzle to beginning of orbit; interorbital width about three-fifths length of orbit; interorbital space flat or slightly concave; tympanic membrane directed laterodorsally, roughly oval in outline, slightly higher than wide, its greatest dimension about one-half length of orbit; no parotoid glands in evidence; angle of jaw below anterior border of tympanic membrane; outline of lower jaw broadly rounded; upper arm mostly contained within body skin; forearm slightly longer than hand; first and third fingers decidedly stouter and longer than second and fourth, tips slightly dilated; fingers in order of decreasing length 3, 1, 4, 2; palm smooth except for a conspicuous elongated inner metacarpal tubercle in line with first finger (occasionally one or two small palmar tubercles); a short web on either side of second finger; body depressed; proximal half of femur included in body skin; femur decidedly longer than tibia; heels not meeting when legs are flexed; tarsus about one-third length of hind foot; sole smooth save for large

external metatarsal tubercle (the digging 'spade') on inner (ventral) border of foot just distal to tarsus; free cutting edge of spade directed lateroventrally; toes in order of decreasing length, 4, 3, 5, 2, 1; web but slightly scalloped; one phalanx free on all toes but fourth, on which two phalanges extend beyond web.

Tongue broad, width more than half that of mouth at angles of jaws, attached to floor of mouth by slightly more than half its length; internal nares large, close to anterior border of upper jaw; vomerine teeth in two oval transverse groups between internal nares.

Back relatively smooth; dorsal surface with many small, low, rounded tubercles, more numerous, larger and higher on sides of body; ventral surface of body smooth or with but few low rounded areolae; buttocks slightly rugose.

Color (in life) above dark green, with scattered spots of dusky; four (or two) incomplete longitudinal stripes of dull white, inner pair in line with inner margins of orbits, the outer in line with tops of tympanic membranes; tubercles on back and sides tipped with red or orange in young individuals; ventral surface plain white; throat region (vocal sac) blackish in males, dusky in females. Females lack the conspicuous longitudinal dorsal streaking of white, this being broken and much less extensive.

MEASUREMENTS OF ADULT SPECIMENS OF *Scaphiopus hammondii* FROM CALIFORNIA

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4435[1]	♀	Jan. —, 1910	51	18.7	22.0	7.8	5.0	13.0	11.0	25.0	20.0	11.5	33
615[1]	♀	Mar. 22, 1909	52	18.0	22.4	7.5	6.0	14.0	13.0	24.5	20.0	11.5	33
4372[1]	♀	Mar. 8, 1911	58	19.0	22.0	7.0	5.0	14.5	13.5	25.5	20.5	12.0	37
616[1]	♀	Mar. 22, 1909	59	21.0	22.3	8.0	5.0	15.5	12.2	26.4	21.0	13.0	34
4371[1]	♀	Jan. —, 1910	61	20.0	24.0	8.0	5.0	16.0	13.0	27.0	24.0	13.0	38
9127[2]	♂	Apr. 10, 1923	46	16.5	19.5	7.3	3.4	13.5	13.0	20.5	18.5	11.0	31
4334[1]	♂	July 4, 1909	52	19.5	23.5	8.5	5.0	15.0	12.5	25.0	21.0	12.0	33
1199[1]	♂	July 4, 1909	55	19.5	23.3	8.0	5.5	14.5	13.5	23.5	21.0	11.5	33
9124[2]	♂	Apr. 10, 1923	56	19.5	22.5	8.0	4.0	13.0	12.0	26.0	20.0	12.5	36

[1] Sierra Madre, Los Angeles Co. [2] Santa Maria, Santa Barbara Co.

Description of larva.—Greatest length of head-and-body 31 mm.; of tail 42 mm.; length of body contained 1.3 to 1.4 times in length of tail; width of body 1.6 in its own length; nares decidedly nearer to orbits than to end of snout; internarial space 1.8 to 2.5 in interorbital space; interorbital space 5.4 to 7.7 in length of head-and-body; tip of snout to orbit about 7 in length of head-and-body; spiraculum sinistral, low on side of body, aperture directed backward and slightly upward, center of aperture slightly forward of or at middle of head-and-body length; anus median, opening at lower edge of ventral fin; greatest height of fins about 2 times in head-and-body length; height of muscular portion of tail at juncture with body about 6 times in

head-and-body length; origin of dorsal fin at about midpoint of head-and-body length; end of snout blunt, anterior part of body bluntly tapered, posterior end squarish, not rounded; external nares and orbits well up on dorsal surface; body depressed, broader than high. General coloration dark brown or blackish, not mottled; ventral surface with bluish (rarely reddish) iridescence; caudal fins transparent.

Mouth region small, papillated part scarcely as wide as interorbital space; larval teeth in $\frac{2}{4}$ rows; first row complete across entire width of mouth region; second, reduced to short lateral row on each side of lower jaw; third row like second, still shorter; fourth like second, each half slightly longer than in second; fifth extending across mouth region, narrowly interrupted medially; sixth a single short central row about as long as lower jaw (text fig. EE).

The following is a list of the specimens of *Scaphiopus hammondii* from California contained in the collection of the Museum of Vertebrate Zoology.

M. V. Z. No.	Locality	Date	Sex	Head-and-body length in millimeters	Remarks
6048	Salmon Ranch, Mono Lake, Mono Co	June 20, 1916		30 0	
5607	sw. side Mono Lake, Mono Co.	July 22, 1915		34 5	
2589	Lane Bridge, 10 mi. n. Fresno, Fresno Co.	Apr. 6, 1911	.	35 0	
2590	Lane Bridge, 10 mi. n. Fresno, Fresno Co.	Apr. 8, 1911	.	45.0	
3729	Benton, Mono Co.	July 7, 1912	.	45 6	
8634	Convict Creek, Long Valley, Mono Co.	July 11, 1922	♂	46 0	Nuptial excrescences developed
6743	1 mi. n. Earlimart, Tulare Co.	May 17, 1918	♀	46 4	Small residue of eggs in ovary
9123	Santa Maria, Santa Barbara Co.	Apr. 10, 1923	♂	47.7	No nuptial excrescences
614	Sierra Madre, Los Angeles Co.	Mar. 28, 1909	♀	51 0	Ovary full of eggs
4335	Sierra Madre, Los Angeles Co.	Jan. —, 1910	♀	51.0	Ovary full of eggs
6046	Farrington Ranch, Mono Lake, Mono Co.	May 5, 1916	♀	51 5	Ovary full of eggs; oviduct swollen
6744	Tipton, Tulare Co.	May 24, 1918	♀	51 5	Ovary full of eggs
615	Sierra Madre, Los Angeles Co.	Mar. 22, 1909	♀	51.7	Ovary full of eggs
4334	Sierra Madre, Los Angeles Co.	July 4, 1909	♂	52 0	Nuptial excrescences developed
4373	Sierra Madre, Los Angeles Co.	May 17, 1912	♂	52 2	Nuptial excrescences developed
4369	Sierra Madre, Los Angeles Co.	May 31, 1908	♀	53 5	Spawned out
6047	Farrington Ranch, Mono Lake, Mono Co.	May 8, 1916	♀	53 0	Ovary full of eggs; oviduct swollen
6049	Salmon Ranch, Mono Lake, Mono Co.	June 20, 1916	♀	54.5	Ovary full of eggs
1199	Sierra Madre, Los Angeles Co.	July 4, 1909	♂	54.8	Nuptial excrescences developed
4372	Sierra Madre, Los Angeles Co.	Mar. 8, 1911	♀	57 8	Ovary full of eggs
616	Sierra Madre, Los Angeles Co.	Mar. 22, 1909	♀	59.6	Ovary full of eggs
4370	Sierra Madre, Los Angeles Co.	June 8, 1908	♀	60 0	Spawned out
4371	Sierra Madre, Los Angeles Co.	Jan. 10, ——	♀	60 0	Ovary full of eggs

The following specimens are in the Museum's collection from eastern Washington, eastern Oregon, and Nevada.

M. V. Z. No.	Locality	Date	Sex	Head-and-body length in millimeters
1568	Quinn River Crossing, Humboldt Co., Nev.	May 30, 1909	♂	43.8
1567	Quinn River Crossing, Humboldt Co., Nev.	June 4, 1909	♀	47.5
7462	Prineville, Crook Co., Ore.	July 24, 1920	♂	49.5
5591	Wallula, Walla Walla Co., Wash.	June 16, 1914	♂	50.8
8902	Bunkerville, Lincoln Co., Nev.	Mar. 28, 1923	♂	51.2
5590	Wallula, Walla Walla Co., Wash.	June 12, 1914	...	54.1
1556	Big Creek Ranch, base of Pine Forest Mts., Humboldt Co., Nev.	June 21, 1909	...	54.5
7551	Thousand Creek Hot Springs, nw. Humboldt Co., Nev.	June 15, 1920	..	55.0
1252	Virgin Valley, Humboldt Co., Nev.	May 21, 1909	....	56.0

History.—*Scaphiopus hammondii* was originally described by Baird in 1859 from a specimen obtained by Dr. J. F. Hammond at Fort Reading [= near Redding], California, during the course of the Pacific Railroad Surveys. Subsequently it was reported from San Diego (Cooper, 1868; Cope, 1883) and Santa Barbara (Yarrow and Henshaw, 1878). Until recently these stations constituted the only two California localities of record for the species. Cope in 1866 sought to establish a separate genus, *Spea*, to include *hammondii* and its varieties, but the characters which he used to distinguish *Spea* from *Scaphiopus* are too slight to warrant the separation. Cope also described several varietal forms of *hammondii* on the basis of material from the Great Basin and elsewhere (see Cope, 1863; Cope *in* Yarrow, 1875; Cope, 1883) but these have not found general acceptance. It is outside the province of the present paper to review these forms; the writer believes that the Great Basin and Rocky Mountain forms may prove to merit recognition, but a careful monographic study of the species is needed to settle the matter.

Range.—*Scaphiopus hammondii*, considering the species in its widest sense, ranges from the western margin of the Great Plains to the Pacific Coast and from the Mexican line across the Canadian boundary. On the east it has been recorded at El Paso, Texas (Strecker, 1915, p. 54); Clarendon, Donley County, Texas (Cope, 1892, p. 332); and in Armstrong County, Texas (Strecker, *loc. cit.*);

Colorado Spring, Colorado (specimens in Mus. Vert. Zool.); Greeley, Colorado (Ellis and Henderson, 1913, p. 52); Green River and Big Horn Basin, Wyoming (Cary, 1917, pp. 19, 27); Camp Thorne [near Glendive], Montana (Allen, 1874, p. 68); Fort Benton, Montana (Cope, 1889, p. 308); and Fort Union [Williams County], North Dakota (Cope, 1863, p. 53). On the north it reaches Vernon, British Columbia (Cope, 1893, p. 182), Blackfoot Fork, Montana, and Walla Walla, Washington (Cope, 1889, pp. 308, 305). On the south it has been found near El Paso (see above), at Alamogordo, Otero County (Stone, 1911, p. 223), and at Santa Fe and Fort Wingate, New Mexico (Cope, 1883, p. 14; Coues, 1875, p. 630); and on the Painted Desert of Arizona (Stejneger, 1890, p. 117). Cope (1887, p. 12; 1889, p. 306) records "a slightly differentiated variety" from Chihuahua and from Guanajuato, Mexico. Schmidt (1922, p. 633) lists one specimen from Ensenada, northern Lower California. According to Stecker (1915, p. 54), Cope records *S. hammondii* from Helotes, Texas. The western localities of record are Wallula, Walla Walla County, Washington, and Prineville, Crook County, Oregon (specimens in Mus. Vert. Zool.), and the California stations given below.

In California this spadefoot has been found at the following localities: near Redding, Shasta County (Baird, 1859*b*, p. 12); Stockton, San Joaquin County (Storer, MS); near Jenny Lind, Calaveras County (Storer, MS); Lane Bridge, Fresno County (Grinnell and Camp, 1917, p. 140); Earlimart and Tipton, Tulare County (Mus. Vert. Zool.); Simmler, San Luis Obispo County (Grinnell and Camp, *loc. cit.*); Santa Maria, Santa Barbara County (specimens in Mus. Vert. Zool.; Storer, MS); Mono Lake and Benton (Grinnell and Camp, *loc. cit.*), and Long Valley and Mammoth, Mono County (Mus. Vert. Zool.); Olancha, Inyo County (Stejneger, 1893, p. 222); Santa Barbara (Yarrow and Henshaw, 1878, p. 209); Los Angeles, and Sierra Madre (Grinnell and Camp, *loc. cit.*), and Altadena, Los Angeles County (Storer, MS); near Banning, Riverside County (Storer, MS); and San Diego (Cooper, 1868, p. 486).

Larvae determined to be of this species have been collected at the following additional localities: Los Angeles (Arroyo Seco and grounds of the Southern Branch of the University of California) and Laguna Cañon above the beach, Orange County.

This spadefoot has never been recorded from either the Mohave or Colorado Desert or the northwestern portion of the Coast Range.

Life-history.—The spadefoot toads represent the most extreme modification among the Salientia of North America toward successful existence under arid conditions. Their requirements with respect to water are reduced to a minimum. Shallow temporary rain pools suffice for the egg and larval stages which are passed through in a remarkably short interval of time. From the time they emerge from the water the adults are provided with cutting 'spades' on the hind feet which enable them to burrow down into the ground and thus to escape desiccation.

Scaphiopus hammondii is the most elusive of the California Salientia. Despite the fact that the species occupies a wide range of territory in the settled portion of the State, very few of the adult animals come to the attention of human beings. Specimens are relatively uncommon in collections as evidenced by the small series listed above, and naturalists who live right in the midst of territory occupied by the species are often completely in ignorance concerning the presence of the animals. That they thus escape observation is due to two traits: the adults are seldom active save under the cover of complete darkness, and the spawning activities may occupy only one or two nights in a year.

Only recently have the real habits of the spadefoot toads been learned. For many years it was believed that the animals spent most of their adult life underground and that they came forth, only at intervals of several years, for spawning purposes. Thus, Dickerson (1906, p. 56) writing of *Scaphiopus holbrookii* of eastern North America, says: ". . . these facts are well authenticated: They disappear with never a stray one left behind, and they may not appear again in the same locality for many years." Recent observations on *S. holbrookii* by Overton (1914; 1915*a*; 1915*b*) on Long Island, New York, and on *S. couchii* by Strecker (1908) at Waco, Texas, have shown that the spadefoots living in those particular localities are in evidence for spawning purposes every year, though for only a very brief period in any one season. The few facts at hand concerning *Scaphiopus hammondii* in California suggest that the same is true with respect to this species. But if the observer does not happen to be on hand *at the right time and in the right place* the animals will escape observation entirely.

The behavior of some adult *Scaphiopus hammondii* collected by the writer at Santa Maria, Santa Barbara County, on April 10, 1923,

may be cited as bearing on the nocturnal activities of this species. These animals were taken alive to Berkeley where they were kept for a month or so in a metal box provided with a layer of earth several inches in depth. At first the box was covered by a glass plate; later, a tight-fitting tin lid was used which excluded practically all the daylight. Examination of the box by day when the glass lid was in use revealed none of the toads and the same was usually true when the tin lid had been down; the spadefoots had burrowed into the dirt. But each night, after dark, they were to be found out on top of the earth. The light of an electric bulb held over the box at night was usually sufficient to stimulate digging movements.

When in the dark the golden-spotted iris of the spadefoot's eye is completely relaxed so that the eye appears entirely black, but within a few seconds after one of the animals has been brought into light of any considerable intensity the iris begins to contract toward a vertical ellipse. In the strong sunlight of midday the aperture is reduced to a narrow vertical slit. I do not recall any other local amphibian which has so pronounced a diaphragm reaction.

No information is at hand to indicate the nature of the retreats occupied by the Western Spadefoot in California. The eastern species (*S. holbrookii*) has been known to excavate short pyriform retreats (Dickerson, 1906, p. 57). An example of *S. hammondii* captured near Santa Maria by Mr. L. N. Crawford on April 14, 1923, was released in the garden of his residence on the morning of April 17. By noon it had dug to a depth of 4 inches; by evening it had gone down too deep to be unearthed.

Most of the Western Spadefoots which have been collected in California have been come upon by naturalists who were in the field immediately following late spring or summer rains when the animals were out to spawn. Occasionally they have been captured in traps set for small mice. In this manner Mr. Joseph Dixon obtained two *S. hammondii* in the vicinity of Mono Lake. In northwestern Nevada, Taylor (1912, p. 345) has reported the capture of one individual in a mousetrap and of two others which were abroad at the breeding season.

The voice of the Western Spadefoot Toad is to be heard only during a brief season each year, when the adults appear aboveground for spawning purposes. Unlike some of our other Salientia, this species does not call over a long period. Camp (MS) records hearing the notes of males in the vicinity of Sierra Madre on March 3, 4, and 6, 1909, on May 11, 1913, and in May, 1914. On July 4, 1909, in the

same neighborhood, he found two males in a reservoir into which a stream of water was running; one was clasping the other and the latter was croaking vigorously. The writer has heard the voice of the Spadefoot on but three occasions, as noted below. Naturalists who are interested in learning more about the spadefoot should go abroad just after heavy rain storms in the late spring months as it is then that the voice of the animal is most likely to be heard.

The notes of the male Western Spadefoot during the breeding season are as loud or louder than those of any of our other native Salientia. They carry well, so that, in open country, it is possible to hear them when the listener is at a distance of half a mile or more from the animals. The individual note is a low-toned rather prolonged *tirr-r-r-r*. One listener compared the note to the noise made by stroking a rosined string attached to an empty tin can; another to the sound produced by a wooden ball falling and bouncing rapidly on a light wooden table. The note has a ventriloquial quality, at least to human ears, and when a person is searching for one of the toads he is apt to have considerable difficulty in determining the exact location of the performer. The female Spadefoot gives only a few muffled notes, much lower than those of the male.

In the pools near Santa Maria, described below, a dozen or more Western Spadefoots were watched and listened to at about 9 o'clock on the night of April 10, 1923. Each of the male toads was distant from his nearest neighbor by a meter or more. All were in the water, sprawled out, with all four legs widely extended and their bodies floating at the surface. The vocal pouch in this species occupies the space under the chin, and when inflated is directed forward, with a slight median constriction (see pl. 10, fig. 28). When the males are on the water the vocal pouch is kept partially distended and at the instant the note is produced the pouch swells far forward. Each note lasts about half a second and when the animals are in full chorus the intervals between successive notes from one toad are about two seconds in duration. Different individuals croak at different times and in slightly different keys so that the effect of the 'chorus,' if such it may be called, is quite varied. Males when grasped across the back between the thumb and forefinger of a person's hand give their notes in rapid succession.

The present writer made a special search for material bearing on the life-history of *Scaphiopus hammondii* at various places in central and southern California during March and early April of 1923, but

found the species in only three localities. Near Banning, Riverside County, on the night of March 24, the notes of one or two individuals of this species were heard coming from a pool of water beside a railroad embankment. This was well after dark (9:15 P.M.) on a clear cold night; there had been no rain for some time previously. The notes were followed up but the surface of the pond was found to be covered with a dense stand of dead weeds and the animals could not be seen. At Altadena, Los Angeles County, a cement-lined reservoir was visited at about 8 o'clock on the night of April 6. Several males were croaking vigorously but they were too far out in the pool to be seen or captured. There had been heavy rains intermittently from March 31 to April 5. When this pool was visited again on April 8, no spadefoots could be heard. Near Santa Maria, Santa Barbara County, spadefoots were found in some numbers on the night of April 10; there had been heavy rain during the night of April 9. No animals were to be heard or seen in the same pools on the night of April 14. One spadefoot was heard in another location near Santa Maria on the night of the fourteenth.

Eggs of *Scaphiopus hammondii* were found in some rain pools about 3 miles southwest of Santa Maria on the afternoon of April 10, 1923. Some shallow depressions in a pasture and the gutter at the side of a country road held water accumulated from the recent rains (April 1 to 9). In no place was the depth of the water greater than 500 millimeters and for the most part it was less than 150 millimeters. In these pools were many egg masses, all of about the same advanced stage of embryonic development, and all attached to vertical stems of grasses and other plants in the water. All were attached below the surface at depths of from 25 to 100 millimeters (estimated). No mass was found at the surface of the water. In some cases a spiral disposition was evident, suggesting that the spadefoots had circled the stem when the eggs were being extruded. In other masses there was no indication of spiral arrangement.

Macroscopically the eggs are somewhat like those of a true frog (*Rana*) and somewhat like those of the Pacific Tree-toad (*Hyla regilla*). There appears to be but a single gelatinous envelope though actually there are two, the inner one being thin and close around the vitelline capsule. There is no general outer covering as on the eggs of *Hyla regilla* and the mass has the outline of a cluster of grapes (see pl. 10, fig. 29; text fig. W). When lifted out of the water the mass naturally droops or lengthens out somewhat, but not so much as an egg mass of *Hyla regilla*.

Counts of contiguous masses in a portion of one pool at Santa Maria gave the following numbers of eggs in separate clusters: 27, 18, 34, 42, 28, 31, 21, 17, 10, 15, 30, 22, 32; maximum 42, minimum 10, average 24. These thirteen masses were all which could be reached from one position in the pool, roughly in a circle about five feet in diameter.

The number of eggs laid by one female is not known. At Waco, Texas, Strecker (1908, p. 202) found that the egg complement of *Scaphiopus couchii* ranged from 343 to 528. From the number of ovarian eggs seen in certain California specimens of *Scaphiopus hammondii* I would judge that a somewhat similar number of eggs is deposited by the latter species. The number of eggs in individual clumps or strings of eggs is much larger for *couchii* at Waco (45 to 124) than for *hammondii* at Santa Maria (10 to 42).

One lot of eggs collected at Santa Maria on April 11, 1923, after preservation in 5 per cent formalin, presented the following measurements (in millimeters):

	Egg	Vitelline capsule	Inner jelly coat	Outer jelly coat
Minimum	1.47	1.50	1.63	3.25
Maximum	1.62	1.75	1.88	3.75
Average of 9	1.60	1.66	1.81	3.60

Another lot also in early stages gave the following measurements:

	Egg	Vitelline capsule	Inner jelly coat	Outer jelly coat
Minimum	1.55	1.66	1.81	3.55
Maximum	1.66	1.77	1.94	4.44
Average of 6	1.62	1.73	1.85	4.07

Ten additional eggs were measured. The results were: minimum 1.55 millimeters; maximum 1.72; average 1.64.

The jelly, when not covered with sediment, is clear and highly transparent. The eggs in the earlier stages of development are dark greenish olive in color.

The material obtained at Santa Maria was in two distinct stages of development, one portion obviously having been laid on the night of April 9 (and 10?) and the other at an unknown earlier date, but probably not earlier than April 3. The latter were nearly ready to hatch; in fact some of the embryos dropped out of the jelly when the latter was handled.

As development proceeds, the jelly swells to larger size than the dimensions given above so that when the embryos are ready to hatch the outer jelly coat is almost twice its original diameter. On the morning of April 11, at 11 A.M., the water immediately about the egg masses was at a temperature of 21.0° C. This relatively high temperature is most certainly a factor in the rapid development of the eggs, but it probably is also dangerous in some degree in that it permits also the rapid development of a fungus which may gain entrance to the vitelline capsules. It was noticed that in masses of eggs advanced in development fully 50 per cent of the eggs had failed to develop or had developed only to a relatively early stage.

The seasonal program of *Scaphiopus hammondii* in California is indicated by the items in the following table. Except as noted, this table is based on material in the collection of the Museum of Vertebrate Zoology.

Locality	Date	Stage of development
Bellota, San Joaquin Co.	March 11, 1923.	Small larvae
Santa Maria, Santa Barbara Co.	Apr. 10–11, 1923.	Eggs in early stages and others ready to hatch
Jenny Lind, Calaveras Co.	Apr. 9, 1922	Large larvae, with hind limbs
Grounds of Southern Branch, University of California, Los Angeles	Apr. —, 1921	Larvae with hind limb buds
Arroyo Seco, Los Angeles	May 3, 1921	Metamorphosing larva
Bellota, San Joaquin Co.	May 8, 1923	Large larvae*
Sierra Madre, Los Angeles Co.	May 11, 1913	Large larvae, some metamorphosing†
Sierra Madre, Los Angeles Co.	May —, 1914	Large larvae, some metamorphosing†
2 mi. w. Sierra Madre, Los Angeles Co.	May 20, 1913	Many larvae, some with hind limb buds just appearing, others with tail practically resorbed
Carrizo Plain, 7 mi. se. Simmler, San Luis Obispo Co.	May 28, 1911	Two young with tail stub less than half length of body
3 mi. e. Whitmore Tub, Long Valley, Mono Co., altitude, 6800 feet	July 12–13, 1922.	Large larvae, some toads completely metamorphosed

* H. J. Snook, in letter; these larvae transformed in the laboratory prior to May 18.
† C. L. Camp, MS.

Additional data, indicating possible dates of spawning, are included in the table of adults given in the earlier part of this chapter.

The larvae of *Scaphiopus hammondii* attain a large size before metamorphosing (pl. 10, fig. 30). The largest specimens at hand, from Long Valley, Mono County, July 13, 1922, measure 71 millimeters in total length. Of this the body length is 31 millimeters and the tail 40 millimeters. Some reduction occurs with metamorphosis, as completely transformed individuals taken at the same time and place measure from 17.5 to 19.2 millimeters in head-and-body length. Recently metamorphosed individuals from other localities range from 16.5 to 31.0 millimeters in head-and-body length.

Spadefoot toads are notable among salientian larvae for leaving the water while the tail is still of considerable size. Two captured on the shore of a pool on Carrizo Plain, San Luis Obispo County, were 29.5 and 31 millimeters in head-and-body length, while their tail stubs measured about 12 millimeters additional. The tadpoles are fairly active in the earlier stages of their development, but after the hind limbs are well developed and until the tail is resorbed they experience some difficulty in maneuvering.

Development is very rapid with all three species of *Scaphiopus*. Overton (1915*b*) found that eggs of *S. holbrookii* laid in pools on Long Island, New York, on August 4 (1915) hatched on August 7, the larvae were almost half-grown by August 14, and fully formed young spadefoots were found in one instance on September 4. Strecker (1908) says of *S. couchii* at Waco, Texas, that the eggs hatch in from 8 to 10 days, the limbs begin to appear on the 20th to 23d day, and on the 27th to 30th day the young leave the water with their tails still in evidence.

The earliest eggs laid at Santa Maria in 1923 hatched in not more than 7 days and probably not more than 5 days. A sample collection of larvae made 17 days after hatching revealed larvae ranging from 18.5 to 43 millimeters in total length. These pools dried up before the larvae underwent metamorphosis, so it was not possible to follow the history through.

The burrowing reflex is manifested as soon as the young spadefoots leave the water. Camp (MS) found that a young individual when placed on a piece of wet bread in strong sunlight at once began to work its hind feet fore and aft in the manner of an adult spadefoot and soon burrowed its way downward and backward into the soft cool substratum. The advantage to the species of the early appearance of

this reflex is manifest. With the drying up of the pools in which the young toads have passed their larval existence, they would quickly be killed by the desiccating influence of the air; by 'digging in' they are able to protect themselves against this calamity.

Larvae of *Scaphiopus hammondii* (considering the species in its broadest sense) have been reported from a number of localities in the western states, though the exact seasonal history has never been followed through in any one place nor have the eggs been described heretofore.

Cope (1883, p. 14) says that in Santa Fe, New Mexico, it was "abundant in July and August when it deposits its eggs in the pools of rainwater. It is very noisy at such times, and the open lots in the city of Santa Fe resound with its cries. They are much like those of the *Scaphiopus holbrookii.*" At Market Lake, Fremont County, Idaho, on August 11, 1876, Cope (1889, p. 308) found "numerous fat larvae of *Spea bombifrons* [= *Scaphiopus hammondii*] occupying small spaces which they had cleared, quite out of reach of the water. Their limbs were nearly full grown, while their tails had suffered no absorption, and their jaws were toothless and cartilaginous; some quite larval in form, others with wider gape. They were engaged in eating the grasshoppers [*Caloptenus spretus,* which were present in abundance] and I detected several specimens with the entire insects in their mouths. In some instances the grasshoppers' bodies were too large and projected from their mouths. These precocious larvae were evidently air-breathers, and hopped about, presenting a curious appearance as they dragged their large tails after them." At Pyramid Lake, Nevada, in July, 1882, Cope (1883, p. 18) found adults in a pond near the lake shore. He states that the adults were very noisy. The same author found the species on the plains east of Fort Benton, Montana (in 1876 or 1882?). Spawning had occurred in water from summer rains which had accumulated in wagon ruts, and the larvae had transformed by August 20 (Cope, 1889, p. 307). Taylor (1912, pp. 345–346) found many larvae in various stages of development in pools on marshy ground at Quinn River Crossing, Humboldt County, Nevada, on June 7, 1909. At Owens Lake, Inyo County, California, adolescents were collected on May 15 and 18, 1891 (Stejneger, 1893, p. 222). Dickerson (1906, p. 60) says that "young specimens were obtained from San Diego, California, in early April. They measure three-fourths inches long, having a blackish skin already covered with reddish warts, and feet that show the black horny spade well devel-

oped. They have the characteristic thick projecting muzzle and obscure tympanum."

Snyder (1920, pp. 83–84) says that in the vicinity of Pyramid Lake, Nevada, *Scaphiopus hammondii* seems to appear regularly each year for breeding. His account is as follows:

I observed them there in 1911, 1912, and again in 1913. They were first seen April 23 to 25, and they were laying eggs May 28 to June 2.

Their appearance was at once announced by a loud chorus which differed markedly from that of *Hyla* or *Rana*, being in a lower key, somewhat guttural, and a little rasping. It was entirely different from that of *Bufo*.

They collected in considerable numbers in the quiet water of irrigating ditches and in little ponds, where at night they sprawled out motionless in the water, their bright eyes projecting just above the surface. When once found they were easily caught, and when placed on the ground they proved to be very slow and awkward little creatures, exhibiting haste only when given an opportunity to sink into the desert sand. . . .

On the evening of June 2, 1911, I happened upon a small pond separated from the water of Pyramid Lake by a narrow bar. The pond was but a few feet in width, and perhaps a hundred feet long. The water was clear and slightly alkaline like that of the lake. In it were hundreds of spadefoots depositing their eggs in masses one layer deep on the upper surfaces of small rocks. The eggs were not piled up after the manner of frogs, nor were they in strings like those of toads. One mass presented fresh eggs and likewise others in which development was marked, plainly indicating that the mass was made of at least two contributions.

During the following night a continued croaking chorus was at times plainly heard, but it ceased at dawn, and shortly after break of day all the toads had disappeared and they returned no more. Diligent search under rocks and in the sand nearby was not rewarded by a single specimen.

The life-history in relation to the environment.—The spadefoot represents the extreme form among the Salientia of California with respect to limited moisture requirements. While it occurs in localities tenanted by other species of tailless amphibians it there occupies the driest local 'niche,' and it is able to live successfully in localities unsuited by reason of moisture deficiency to other species. The principal features which enable *Scaphiopus hammondii* to do this are the possession of digging equipment in the form of 'spades' on the hind feet and the instinctive use of these in excavating a subterranean retreat in which to take shelter to avoid desiccation. *Bufo b. halophilus* lives in localities tenanted by *Scaphiopus*, but the former is not able to excavate in the manner of the latter. Of the desert-inhabiting toads, *Bufo cognatus* has a development of metatarsal tubercle comparable with that of *Scaphiopus*, which suggests that it also may be able to burrow as a safety measure. An apparent anomaly is seen in the relatively smooth skin of *Scaphiopus*. Other species of terrestrial

amphibians inhabiting relatively arid situations possess a thickened and roughened integument. I believe that the smooth surface texture of the skin of *Scaphiopus* (which is carried to an extreme on the soles of the hind feet) is related to facilitating movement through the earth when burrowing. The surface texture of the skin of *Scaphiopus* compares rather favorably with that of several of the aquatic frogs; reduction of friction in earth and in water would seem to be a factor here.

Scaphiopus, in combination with its digging equipment, has other characteristics which would seem to be of decided benefit to an amphibian living amid arid surroundings. The voice of the male at spawning time is very loud, equaling or exceeding that of *Hyla regilla* and many times stronger than that of *Bufo b. halophilus.* Upon the advent of rain in amount to form pools we may expect that the first male *Scaphiopus* to enter a rain pool would begin calling; this would serve to attract females and other males so that a breeding colony would be established quickly. Rain pools do not necessarily always form in the same place in successive years. If, as we have reason to suppose, the adults are more or less scattered when in their burrows, the strong voice of the first male entering a pond suitable as a breeding environment would serve to concentrate the local population there. Once concentrated, spawning is evidently accomplished with speed as indicated by the large numbers of eggs in similar stages of development found in the ponds near Santa Maria following the *first heavy late spring rain.* The embryonic developmental period is found to be short. The larval period is probably also short if we may judge by analogy from the known facts in the case of the other two widely distributed species of *Scaphiopus* in the United States. The newly transformed young spadefoot has at once the burrowing reflex of the species, which it must, in the case of prairie ponds lacking a border of aquatic vegetation as temporary shelter, put to immediate use to protect itself from desiccation.

Scaphiopus hammondii has penetrated to the northern end of the semi-arid area in interior California (head of the Sacramento Valley), to the northern end of the Great Basin (southern British Columbia), and along the eastern base of the Rockies to eastern Montana. It occupies the entire area where open-surfaced rain pools are likely to occur. No spadefoot seems to have been found on the Great Plains of middle North America. The deserts of California (Mohave and Colorado) seem at the present time to be untenanted by spadefoots of any

species. The sandy texture of the soil in many places and the fact that rain pools seldom form there are possibly the excluding factors. The presence of alkali sinks indicating the former occurrence of lakes in that region has been taken by some climatologists to mean that a cycle of increasing aridity is claiming the region, in which event conditions on those areas are growing less and less favorable for amphibians, even of the extreme type of *Scaphiopus*. The species probably occurred there when the lakes were in existence, as alkali alone, even in high concentration, does not seem to be a deterrent to this spadefoot.

Bufo alvarius Girard. Colorado River Toad

(Pl. 12, fig. 32)

Bufo alvarius Girard *in* Baird (1859*a*, p. 26, pl. 41 [figs. 1–6]). Original description, type from Valley of Gila and Colorado [= Fort Yuma, California; see Cope, 1889, p. 267].

Bufo alvarius, Cooper (1868, pp. 485–486; 1869, p. 480). Colorado River Valley.

Bufo alvarius, Cope (1889, pp. 265–267, text fig. 62). General account.

Bufo alvarius, Dickerson (1906, pp. 106–108, col. pl. 5, pls. 36, 37). General account.

Bufo alvarius, Camp (1915, p. 509). Colorado River Valley.

Bufo alvarius, Grinnell and Camp (1917, p. 144, fig. 4). Range in California.

Bufo alvarius, Stejneger and Barbour (1917, p. 26; 1923, pp. 23–24). General range.

Diagnosis.—Size very large, largest of the north American bufonids, head-and-body length up to 130 millimeters ($5\frac{1}{8}$ inches) (Ruthven [1907, p. 505] lists a specimen 147 mm. long); skin smooth and leathery; warts on body small, low, and scattered; cranial crests curved around eyes; parotoids long and divergent posteriorly; large raised 'warts' or glands on exposed surface of femur and tibia.

Comparisons.—Distinguished from other California Salientia (except Bufonidae) by large size and presence of distinct parotoid glands on shoulder region; from all other California Bufonidae by large size, curved cranial crests, very smooth skin, and large glands on femur and tibia.

Description.—Size very large, general build stout, head and body depressed. Outline of head from above, acuminate oval, muzzle bluntly rounded in profile, tip flat-topped; canthus rostralis very distinct, slightly shorter than length of orbit; external nares nearly terminal, below canthus rostralis; orbit rounded; eyelids thick; interorbital space about three-fourths length of orbit; each cranial crest a single curved ridge paralleling median and posterior margins of orbit, ending just above tympanic membrane; preorbital crest straight; occasionally a transverse postorbital crest between tympanum and orbit;

tympanic membrane oval, smaller than orbit, horizontal axis about four-fifths vertical axis; parotoid glands twice as long as broad, descending on shoulders, length about 1½ times length of orbit; angle of jaw below tympanic membrane; head one-third wider than long; gular fold slight; forearm longer than hand; inner finger stoutest; two flattened metacarpal tubercles, both large but inner smaller than outer; subarticular tubercles low; fingers in order of decreasing length, 3, 1, 2, 4; back very flat; hind limb stouter than fore limb; femur about equal to tibia in length; tarsus about two-fifths length of whole foot; foot relatively short; inner metatarsal tubercle large and rounded, outer one small and flattened; toes in order of decreasing length, 4, 3, 5, 2, 1; web deeply scalloped, margin between third and fourth toes opposite first phalanx of latter.

Outline of lower jaw broadly oval in adults, more acute in young; tongue thin, oval in outline, width about half that of mouth, attached by less than half its length to floor of mouth; internal nares pyriform, located far forward in anterior part of mouth.

Body everywhere nearly smooth, skin leathery in texture; a few low warts on eyelids and interorbital region; parotoid glands smooth-surfaced; several large warts posterior to mouth in line with commissure; few very small, low, scattered warts on back; sides of body areolated; ventral surface smooth anteriorly, roughened from throat region posteriorly; few warts on upper arm and dorsal surface of hand; one large raised gland on anterodorsal surface of femur and several on exposed surface of tibia.

General coloration on upper and lateral surfaces of body and limbs, grayish or brownish green of light or dark shade; small warts orange, sometimes rimmed with dusky; ventral surface dingy white; fingers and toes tipped with dark reddish brown or blackish; iris of eye light or dark metallic yellow, prominently veined with red; pupil horizontally oval, black (description of coloration adapted from Dickerson, 1906, p. 106).

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo alvarius* FROM CALIFORNIA AND ARIZONA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
3738	♀	Holtville, Imperial Co., Calif.	June 2, 1912	117	33	45 0	13.0	9 0	30.2	23.0	40.2	40 7	28.5	63
8264	♀	Mohave [=Ft. Mohave], Ariz.	[1861]	129.5	40.8	58.0	16 0	12 0	35.0	32 0	48.0	48.5	33.5	77
7703	♀ ?	6 mi. n. Tucson, Pima Co., Ariz.	Sept. 7, 1919	130	35	46.0	13.2	10.0	31.0	24.5	49.0	44.0	29.0	70
3736	♂	Meloland, Imperial Co., Calif.	June 18, 1912	120	34	45.0	13.0	10.0	32.0	27.5	46.0	45.0	29.0	66
8265	♂	Mohave [=Ft. Mohave], Ariz.	[1861]	124	40.4	52.5	15 5	11.0	37.0	27 0	57 0	48.0	30.5	76
8179	♂	Tolladay's Well, Maricopa Co., Ariz.	July 16, 1921	132	41	50.0	17.0	11.0	30.0	28.0	50.3	48.5	33.0	76

History.—*Bufo alvarius* was originally described from a single specimen said to have been obtained in the "valley of the Gila and Colorado," but which, according to Cope (1889, p. 267), was actually collected at Fort Yuma, California.

Range.—This distinctive species is restricted in its range to southern Arizona and southeastern California. The easternmost locality of record in Arizona is for Tucson, Pima County (Ruthven, 1907, pp. 505–507). Elsewhere in that state it has been found at Phoenix (Dickerson, 1906, p. 107; Van Denburgh and Slevin, 1913, p. 395), Tolladay's Well (specimen in Mus. Vert. Zool.), and Sentinel, Maricopa County, and at Maricopa, Pinal County (Stone, 1911, p. 223). Many specimens of the species were obtained by Slevin at Yuma, Arizona, September 10 to 21, 1912 (Van Denburgh and Slevin, *loc. cit.*). Cooper (1869, p. 480) mentions the species as occurring at Fort Mohave, Colorado Valley [= Arizona]. The specimens which formed the basis for this record have been in the Department of Zoology of the University of California for many years and are now in the collection of the Museum of Vertebrate Zoology of that institution (nos. 8264, 8265). *Alvarius* has been found in the Imperial Valley of California at Meloland (Grinnell and Camp, 1917, p. 144) and at Holtville. It quite probably has spread to other nearby localities in Imperial Valley; for as noted below the species is more aquatic than most bufos and it is therefore more likely to be dispersed by water movement in irrigation canals.

Life-history.—Despite the fact that this is the largest toad in America north of Mexico and hence deserving of special attention for this reason alone, very little is known of its habits. Cooper (1868, p. 486) says that in the Colorado River Valley it has somewhat the habits of a frog. He reports (1869, p. 480) meeting with this species on May 28, 1861, at Fort Mohave, Arizona, where he describes it as "an enormous semi-aquatic species nearly as smooth as a frog." At Meloland, in the Imperial Valley, two individuals were dislodged in a field where some barley was being harvested on June 18, 1912. Another individual was taken under an electric light in Holtville at 8 o'clock on the evening of June 2, 1912. Accompanying the latter specimen is a note which states that the animal "ran" instead of hopping in the usual manner of a toad (Mus. Vert. Zool.).

Ruthven (1907, p. 506) gives the following concerning the life-history of *Bufo alvarius* at Tucson, Arizona, as observed by Professor J. J. Thornber of the University of Arizona.

It is abundant in Tucson and on the University campus. One usually sees the toads a few days before the beginning of the summer showers, and their presence is taken as a sign of rain. Seldom does one see them during dry periods. They may, however, be observed about irrigation ditches and in irrigated land any time during the growing season.

With the first heavy summer showers, as a result of which water will stand in pools, these frogs [sic] appear in abundance and lay eggs which hatch very soon; the young pass in a remarkably short time through the tadpole stage. I do not think it is more than a month's time from the egg stage to the time when the young toad hops away with his tail nearly absorbed.

One particular specimen

was collected in Sabino Cañon, St. Catalina Mts., in June (about the 15th), 1903. A small stream of water came down from the mountains as the result of rain above, and these toads appeared in abundance, pairing almost immediately. On that day every female was laying eggs. The eggs were laid in the clear stream of water, which was perhaps a foot to eighteen inches deep. I assure you there was no lack of noise that day or night, the croaking being incessant. I have also seen it at Oracle, Ariz., where it gets into the sheep troughs and causes more or less trouble.

The life-history in relation to the environment.—This species is distinctive among the Salientia of North America (north of Mexico) in being the largest species of *Bufo* found here and at the same time being restricted in general range to the hottest portion of the continent. So far as known, however, it does not inhabit the desert proper but is to be found only in localities where the water supply is permanent as along large rivers or in irrigated districts. Furthermore, it departs from the typical habits of the toads (*Bufo*) in being semi-aquatic. Three other species of *Bufo* inhabit the general territory occupied by *alvarius*; of these, *punctatus* is of small size and can therefore find safe shelter in small crevices adjacent to seepage or about springs; *cognatus* and *woodhousii* are possessed of tough roughened skins which probably resist desiccation; being of 'average' toad size they can probably find suitable shelters just as do toads in more temperate regions, and they have enlarged metatarsal tubercles suitable for digging. *Alvarius* is of such large size that an adult would probably experience difficulty in securing shelter in the usual bufonine way, were it of terrestrial habit. But by assuming a semi-aquatic mode of life and restricting its range to the neighborhood of permanent streams, it greatly reduces the danger of desiccation. With the bufonid protection of parotoid glands, which, probably by reason of the poisonous nature of their secretion, confer an unusual measure of safety upon the individual, in combination with aquatic habits, a basis

is afforded whereby growth to large size is possible. *Bufo alvarius* may be compared with *Rana catesbeiana* in its large size, smooth skin, and aquatic habits, and the parallel in form is probably related in some degree to the similarity in mode of life of the two species.

Bufo boreas boreas Baird and Girard. Northwestern Toad

Bufo boreas Baird and Girard (1852*b*, pp. 174–175). Original description, type from Columbia River and Puget Sound.

Bufo columbiensis, Baird (1859*b*, p. 12). On Upper Pit River.

Bufo halophilus, Yarrow and Henshaw (1878, p. 208), part. At Lake Tahoe.

Bufo boreas, Boulenger (1882*a*, p. 296), part. General account.

Bufo halophilus, Yarrow (1883, pp. 23, 162), part. Locality records.

Bufo microscaphus, Yarrow (1883, pp. 23, 163). Locality records.

Bufo boreas boreas, Camp (1917*b*, pp. 116, 117). Critical; range.

Bufo boreas boreas, Grinnell and Camp (1917, p. 143, fig. 4). Range in California.

Bufo boreas boreas, Stejneger and Barbour (1917, p. 27; 1923, p. 24). General range.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo boreas boreas* FROM MODOC COUNTY, CALIFORNIA

M. V. Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot	Spread of hind foot
2103	♀	Goose Lake Meadows, near Sugar Hill, 4800 ft.	May 29, 1910	85 5	21 0	36 3	10 5	..	25 7	22.3	35 0	33 0	21.1	54	29
2105	♀	Sugar Hill, 5000 ft.	June 7, 1910	90 5	24 7	34 5	10 5	8 0	27.7	22 7	37 5	32.0	23 2	61	34
2134	♀	Dry Creek, Warner Mts., 4800 ft.	July 30, 1910	103 5	27 8	40 0	11 8	7 0	32 4	35 5	42 8	36 9	26 4	64	38
2107	♀	Goose Lake Meadows near Sugar Hill, 4800 ft.	June 1, 1910	111.0	28 5	43 4	11.5	9 0	31 0	27 4	42 9	40 0	27.6	72	42
2102	♀	Goose Lake Meadows near Sugar Hill, 4800 ft.	May 27, 1910	112 5	26 0	42 0	12 3	9.6	33.7	30.5	46.0	40 2	27.1	71	41
2125	♂	Parker Creek, Warner Mts., 7300 ft.	July 7, 1910	79.0	21.7	28.8	9 6	5.4	23.8	23 0	34.0	30 0	21.3	53	28
2109	♂	Parker Creek, Warner Mts.	June 22, 1910	96.0	25.5	37.4	11 0	7 0	29.7	26 0	42 0	36 5	25 0	66	39
2112	♂	Parker Creek, Warner Mts.	June 19, 1910	97.3	27.0	36.3	10.8	6 4	32.1	24 6	40 0	35.8	25 3	68.5	38
2113	♂	S. fork Pit River near Alturas	June 9, 1910	98.4	24.6	34.5	12.0	7 0	31 0	24.0	38 8	36 5	23 7	64	37
2104	♂	Goose Lake Meadows near Sugar Hill, 4800 ft.	May 29, 1910	99.5	26.0	37.5	10.9	.....	31.8	25 5	37.7	37.3	26 4	68	41

Diagnosis.—As for *Bufo boreas halophilus* (which see), but extreme size larger (up to 112.5 millimeters, 4½ inches), skin rougher between warts, black markings more numerous between warts on back, and spread of hind foot between tips of first and fifth toes usually more than 36 per cent of body length.

Comparisons.—See *Bufo boreas halophilus.*

History.—This toad was originally described by Baird and Girard in 1852 from specimens obtained in Oregon or Washington. The following year other material from the same general region was given the name *Bufo columbiensis* and this name was used for many years. Recently (Camp, 1917*b*) it was shown that the two names applied to one and the same form. Cope in 1866 gave the name *Bufo microscaphus* to a form of the present group; the same author's *Bufo pictus* originally described in 1875 (Cope *in* Coues, 1875), without definite locality, was later stated (Cope, 1889, pp. 269, 270) to be a young individual of this form.

Range.—This northern form of the toad of the Pacific Coast occupies a much wider extent of territory than its relative in central and southern California. Specimens typical of *boreas* are on record in California from Eureka, Humboldt County, Sisson, Siskiyou County, and Mono County (Camp, 1917*b*, p. 116). It occurs in the Sierra Nevada in the vicinity of Lake Tahoe, 6200 feet (Yarrow and Henshaw, 1878, p. 208), on Warner Creek near Mount Lassen at 8000 feet, and in the Warner Mountains in Modoc County up to 8700 feet altitude on Warren Peak (Mus. Vert. Zool.). In Nevada it has been taken at Reno (Mus. Vert. Zool.), in the Pine Forest Mountains, Humboldt County, up to 8500 feet (Taylor, 1912, pp. 343–344), and at Elko, Elko County (Van Denburgh and Slevin, 1921*a*, p. 29). In Utah it has been recorded at Fort Douglas, Salt Lake County, and at various localities in the Wasatch Mountains, Wasatch County, up to an altitude of 8728 feet in Big Cottonwood Cañon (Van Denburgh and Slevin, 1915, p. 101). In Colorado it was first listed by Yarrow (1875, p. 523) under the name *Bufo microscaphus* from South Park; Young (1909, p. 298) recorded it on the east slope of the Rockies (the "Front Range") on Arapahoe Peak, "28 Kilometers west of Boulder," Boulder County. In the western part of Colorado it occurs south to Grand Mesa (Ellis and Henderson, 1913, p. 53). It has been recorded north in the interior "on the Yellowstone" [in Montana?] and at "Chief Mountain Lake" [= Waterton Lake, Alberta] (Coues and Yarrow, 1878, pp. 288–289). In British Columbia it has been

found at and near Hazelton on the Skeena River and at Telegraph Creek on the Stikine River, and is present at Masset, Queen Charlotte Islands (specimens in Mus. Vert. Zool.). In southeastern Alaska it has been taken at numerous localities north to Prince William Sound (Van Denburgh, 1898, p. 139; specimens in Mus. Vert. Zool.). Within the area indicated, west to the Pacific Coast it is the only species of *Bufo* present. In Colorado it is stated to occur only in the mountains. In California it ranges from sea level, as at Eureka, to 8700 feet as in Modoc County. In British Columbia and southeastern Alaska it apparently occurs only at low altitudes.

Life-history.—Few data are at hand concerning this subspecies. Cope (1883, p. 18) states that at Pyramid Lake, Nevada, in July, 1882, toads of this form were "in voice" in a pond near the shore of the lake, suggesting breeding at a later date than with *halophilus* in California. The breeding season of *boreas* in the Rocky Mountains must of necessity be later than in the low altitudes in northern California and Oregon.

Reporting the results of a trip to Klamath and Silver lakes, Oregon, and the lakes in northeastern California, Cope (1883, pp. 19–20) said of this toad:

> It is especially numerous at Klamath Lake, where it covers the basaltic blocks which lie partially in the water, concealed by the *Typhae*, which grow from the bottom. They accumulate there in large piles, sometimes as large as a bushel-measure, and afford abundant food for the *Eutæniæ* which are scarcely less abundant. One specimen of this toad was as large as the average *Bufo marinus* of Brazil, and a specimen seen at Warner's Lake was but little smaller.

Coues and Yarrow (1878, p. 289) say that in Montana "specimens were taken from the stomach of *Salmo namaycush* and other fish of the same genus in this locality, further indicating its aquatic nature."

Bufo boreas halophilus Baird and Girard. California Toad

(Pl. 12, fig. 33; pl. 14, figs. 43, 44; text figs. J, X, FF)

Bufo halophila Baird and Girard (1853*a*, p. 301). Original description, type from Benicia, Solano County, California.
Bufo halophila, Girard (1854, p. 87). Redescription.
Bufo halophila, Girard (*in* Baird, 1859*a*, p. 26, pl. 16 [figs. 7–12]).
Bufo halophilus, Yarrow and Henshaw (1878, p. 208), part. Locality records.
Bufo halophilus, Boulenger (1882*a*, pp. 295–296, 1 fig.), part. General account.
Bufo boreas, Boulenger (1882*a*, p. 296), part. General account.
Bufo halophilus, Yarrow (1883, pp. 23, 162), part. Range.

Bufo halophilus, Townsend (1887, p. 241). At Baird.

Bufo columbiensis, Cope (1889, pp. 267–271, text figs. 63–64), part. General account.

Bufo halophilus, Stejneger (1893, p. 220, pl. 3 [figs. 3*a-b*]). Locality records.

Bufo boreas nelsoni, Stejneger (1893, pp. 220–221, pl. 3 [figs. 4*a-b*]), part. Locality records.

Bufo halophilus, Dickerson (1906, pp. 113–116, pls. 41–43). General account.

Bufo columbiensis, Mearns (1907, pp. 133, 138).

Bufo halophilus, Storer (1912, pp. 89–91, 1 fig.). General account; food.

Bufo columbiensis, Hurter (1912, p. 67). In Orange County.

Bufo boreas halophilus, Camp (1917*b*, pp. 115–117). Critical; range.

Bufo boreas halophilus, Grinnell and Camp (1917, pp. 142–143, fig. 4). Range in California.

Bufo boreas halophilus, Stejneger and Barbour (1917, p. 27; 1923, p. 24) General range.

Bufo boreas halophilus, Grinnell and Storer (1924, pp. 655–657, pl. 60*a*). In Yosemite region.

Diagnosis.—Size large, head-and-body length up to 109.5 millimeters (4⅜ inches); form stout; no cranial crests (occasionally developed in large individuals); skin only slightly roughened between warts; parotoid glands moderate, slightly greater than orbit in length; warts rounded; metatarsal tubercles blunt; spread of hind foot from tip of first toe to tip of fifth toe usually less than 36 per cent of head-and-body length.

Comparisons.—Distinguished from other California Salientia except Bufonidae by well developed parotoid glands; from *Bufo alvarius, cognatus*, and *woodhousii* by absence of cranial crests, from *Bufo punctatus* by larger size and by larger, higher and rounded warts; from *Bufo canorus* by longer parotoid glands separated by more than width of one gland, by larger size, and by different pattern of coloration; from *Bufo boreas boreas* by smaller adult size, lesser spread of hind foot, and by lighter coloration dorsally with few or no dark speckles between black markings on dorsal surface.

Description (based on fully adult specimens from southern and central California listed in tables of measurements).—Size large, form stout, limbs short and stocky; muzzle truncately oval in outline from above, truncate in profile; external nares nearly terminal, opening laterally or anteriorly; canthus rostralis passing above external naris, its length about two-thirds that of orbit; orbit moderate, about one-half length of head; interorbital region concave, width varying from less than half to more than two-thirds length of orbit; cranial crests usually absent [occasionally developed in large individuals, for example, no. 4133, Mus. Vert. Zool.; crests then rectangular, longitudinal elements strictly parallel between orbits, transverse element of each running laterally to above tympanic membrane]; parotoid glands low, irregularly oval in outline, slightly posterior to orbits, placed well down on side of neck region and separated by 1¼ to 1¾ times length of orbit; tympanic membrane below anterior part of parotoid gland, broadly oval or nearly round in outline, longer axis vertical and about two-thirds length of orbit; lower jaw bluntly oval, sometimes

truncate at tip; angle of jaw below middle or posterior margin of orbit; no vocal sac in evidence externally on male; body heavy, slightly longer than wide, flat; fore limb heavy, particularly in males; about one-half of upper arm buried in skin of body; forearm stouter than upper arm in males, about equal in size in females; hand about three-fourths length of forearm; two metacarpal tubercles, one in center of palm, second and smaller one on proximal side of first finger; sub-articular tubercles numerous, a large one opposite end of first phalanx of each finger; digits blunt-ended, subequal in length, in order of decreasing length, 3, 2, 1, 4, inner one stoutest, especially in males; hind limb very stout; femur almost entirely buried in skin of body; tibia usually somewhat shorter than femur; hind foot about two-thirds length of head-and-body; tarsus comprising less than two-fifths length of foot; two large blunt metatarsal tubercles, outer one rounded, inner with a free blunt end; subarticular tubercles numerous and conspicuous; toes rather slender, in order of decreasing length, 4, 3, 5, 2, 1; web large for a toad, extending to tips of all toes, scalloped to middle of first (basal) phalanx on fourth toe.

Tongue oval, broader behind, width about one-half that of jaws at angle of mouth, attached to floor of mouth for slightly more than half its length; internal nares roundedly oval, placed far forward in mouth in females, slightly back from jaw in males.

Tip of nose and margin of upper jaw smooth; upper surface of head, eyelids, dorsal surface of body and exposed surfaces of limbs with numerous blunt warts of varying size (up to 4 mm. in diameter) rounded or oval in outline; between these, many fine pointed warts on females, few or none on males; lateral surface of body between limbs, abruptly areolar, divisions less than 2 mm. in diameter, a small raised point in center of each areola; ventral surface of body and concealed surfaces of limbs smoothly areolate, with a fine point in center of each areola; plantar surfaces of feet with small warts, these more pointed on hind limb; an enlarged wart often present on exposed surface of tibia.

General ground color of exposed portions of body light green, yellowish green, or greenish brown; brownish tinge lacking in males, at least during breeding season; vertebral stripe 3 to 1 mm. in width, yellowish white; dorsal warts dark brown, surrounded individually or in groups by broad areas of black; little or no linear arrangement of warts or black areas; parotoid glands brown like dorsal warts; small warts on areolae of flanks, yellow or orange; ventral surfaces clay colored or dirty white, blotched irregularly with black in some individuals, plain colored in others; exposed surfaces of hands and feet, dark gray; larger tubercles on plantar surfaces yellowish brown; nuptial excrescences on inner three fingers of males dark reddish brown (color description based on lot of twelve pairs of live adults collected near Oakland, April 16, 1912).

Description of larva.—Greatest length of head-and-body 23 mm.; of tail 33 mm.; length of body contained about 1.5 times in length of tail; external nares nearer to orbit than to tip of snout; internarial width about 1.2 times in interorbital width; interorbital width 7 to 9 in length of body; orbit about 25 per cent of body length from tip of snout; spiraculum sinistral, aperture directed backward and upward,

center of aperture behind midpoint of body; anus median; greatest depth of tail (over fins) 3 in its own length; muscular part of tail at base about 2 in greatest height over tail fins; body depressed, decidedly wider than high, broadest between orbit and spiracle, acutely tapered behind; dorsal crest of caudal fin originating at upper base of tail. Labial teeth in $\frac{2}{3}$ rows, first row longest, extending entirely across mouth region; second interrupted medially; third, fourth, and fifth successively shorter but not divided at center; one row of papillae along either side of mouth region (text fig. FF). General coloration dull blackish, or dusky, with no red or yellow; undersurface slightly paler, but with little or no iridescence; tail fin clouded, but without spots; muscular portion of tail solidly blackish; iris black.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo boreas halophilus* FROM SOUTHERN AND CENTRAL CALIFORNIA

M. V. Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot	Spread of hind foot
4341	♀	Sierra Madre, Los Angeles Co.	Apr. 11, 1909	75.0	21.0	30 0	10 0	6.5	21 0	18.7	31 2	26.5	18 3	50	26
4342	♀	Sierra Madre, Los Angeles Co.	Apr. 11, 1909	79 5	22.0	30.5	10 3	6.5	22 5	20.0	29 0	28.5	18.5	50	28
4351	♀	Sierra Madre, Los Angeles Co.	Dec. 3, 1910	85 0	23.0	31.4	10.4	6.3	24 2	18 0	36.0	30.3	20 0	55	27.5
6876	♂	Los Angeles, Los Angeles Co.	Dec. 6, 1917	86 4	23.4	34.0	12.0	5.0	29 0	20.0	32 0	32.8	22.2	60	30
4846	♂	1½ mi. s. El Monte, Los Angeles Co.	July 23, 1913	87.5	25.0	33 3	11.5	5.6	26 5	19.6	36.0	31.5	20.0	54	28
6879	♂	4½ mi. n. Lankershim, Los Angeles Co.	Mar. 14, 1918	87.5	25.0	33.7	11.5	6.4	26 0	21.0	37.6	34 0	22 5	60	31
6878	♂	4½ mi. n. Lankershim, Los Angeles Co.	Mar. 14, 1918	89.5	25 0	34 0	11 0	6.4	26.0	19.3	33 5	31 5	21.0	57	28
6880	♂	4½ mi. n. Lankershim, Los Angeles Co.	Mar. 14, 1918	96 6	26 0	35.0	11 4	7.3	29.2	20 0	41.2	34 5	21.4	59	34
4053	♀	2 mi. sw. Walnut Creek, Contra Costa Co.	July 12, 1912	85 0	21.5	32.5	9.1	7.4	22.0	20.5	30.4	28.2	19 0	54	26.5
4051	♀	Rumsey, Yolo Co.	June 27, 1912	89 3	24.6	36.7	11 2	7 5	24.0	22.6	38.5	31.6	22 7	58	27
4056	♀	2 mi. sw. Walnut Creek, Contra Costa Co.	July 17, 1912	94.0	24.0	34.3	9.5	7.4	24.3	23.2	36.0	31.5	22 1	57	26
4055	♀	2 mi. sw. Walnut Creek, Contra Costa Co.	July 13, 1912	98 0	25.2	38.0	11.5	8.2	27.5	23.6	40.4	35.4	23 0	63	32
4133	♀	Monte Rio, Sonoma Co.	Oct. 15, 1912	109.5	30.4	41.0	11.7	9 3	32 8	25 0	44.3	38.0	26 2	65	34
5024	♂	Gualala River, Sonoma Co.	July 4, 1913	78.2	21.4	28 5	9.0	5.3	22.3	18.1	28.5	27.3	18.4	50	25
5023	♂	Gualala River, Sonoma Co.	July 4, 1913	79.5	22.6	28.0	10 1	6 0	23.6	17.4	28.5	27.5	19.0	52	24
4134	♂	Monte Rio, Sonoma Co.	Oct. 15, 1912	83 0	22 5	30.5	9 0	7 3	22 0	21.0	35.4	30 2	20 5	57	29
4853	♂	San Geronimo, Marin Co.	Apr. 23, 1913	86.4	24 0	30.0	9.7	6.7	23.5	21 2	32.0	33.0	22.0	58	30
4054	♂	2 mi. sw. Walnut Creek, Contra Costa Co.	July 12, 1912	88.5	23.2	32 7	9.2	6 5	27.0	20.0	35.8	32.3	21.6	58	30

History.—*Bufo halophila* was described from a specimen collected by Dr. John L. LeConte at Benicia in August, 1850. A note accompanying the original specimen said "frequenting the edges of the sea [= Carquinez Strait] and jumping into the water when pursued" was probably responsible for the choice of species name. For many years the names *boreas, columbiensis,* and *halophilus* were applied in varying combinations to the toads of western North America. Camp (1917*b*, pp. 115–116), in a critical study of this group which included examination of the types in the National Museum, concluded that *columbiensis* was a synonym of *boreas* and that only two recognizable forms, *boreas* and *halophilus* occur in California. The status of *Bufo boreas nelsoni* Stejneger (1893, pp. 220–221) with respect to California I am unable to determine at the present time; Stejneger and Barbour have omitted it from the second edition (1923) of their check list.

Range.—This toad inhabits the greater part of California, being absent only from the southeastern deserts and from the higher parts of the central Sierra Nevada. At the south it has been found at Ensenada (Van Denburgh and Slevin, 1921*c*, p. 53), and La Grulla, Lower California (Schmidt, 1922, p. 634). The eastern boundary of its range in California is marked by the following stations of occurrence: near Mountain Spring (Storer, MS) and at Vallecito and La Puerta, San Diego County (Grinnell and Camp, 1917, p. 142); in the San Jacinto Mountains at Tahquitz Valley, 8000 feet, and Round Valley, 9000 feet (Mus. Vert. Zool.); at Cabezon, 1700 feet (Mus. Vert. Zool.), Riverside County; in the San Bernardino Mountains at Doble, 7000 feet (Mus. Vert. Zool.), at Victorville, San Bernardino County (Grinnell and Camp, *loc. cit.*); in Kern Valley at Weldon and Onyx (Mus. Vert. Zool.); in Owens Valley north to Independence (Stejneger, 1893, p. 220). In the southern Sierra Nevada it ascends to high altitudes, as to Whitney Meadows [9800 feet], and Round Valley, 10,000 feet, Tulare County (Stejneger, 1893, p. 220). Along the west flank of the Sierra Nevada *halophilus* occurs on the Kings River at 5200 feet (Stejneger, *loc. cit.*), and in Yosemite Valley, 4000 feet (Grinnell and Storer, 1924, p. 655). Westward and northward *halophilus* is found practically everywhere, to the belt of territory where it intergrades with *boreas.* Specimens from Sonoma, Butte, and Inyo counties are the northernmost showing the typical form of subspecies *halophilus.*

Bufo halophilus is a common species throughout its range and except for a few localities in southern California where its range covers that of *Bufo cognatus californicus,* it is the only species of *Bufo* present. *Halophilus* occurs down close to the seacoast, for example just above the ocean beach in San Diego County and near the Hopkins Marine Station at Pacific Grove, and ranges widely in the foothills and valleys of the State, even to high altitudes in the southern Sierra Nevada. Nominally its range includes the Lower Sonoran, Upper Sonoran and Transition zones, but in the vicinity of Mount Whitney it occurs in association with plants and vertebrates characteristic of the Canadian and Hudsonian zones.

Life-history.—This species does not differ markedly in habits from other toads inhabiting north temperate latitudes. *Halophilus* spends the day in any sort of convenient shelter, such as a squirrel or gopher burrow, under a wooden or cement walk, beneath a horse trough, in a bed of leaves, in a road culvert—in short, in any place where it can find retreat from the dry air of midday. In the lowland parts of its range the toads of this species are active throughout the year, with no hibernation such as is practiced by *americanus* in the eastern states. Thus individuals of *halophilus* have been seen abroad at Berkeley in December, and in Solano County four individuals were found active on December 24, 1922. At the higher altitudes in the mountains of southern and central California a dormant period is probably the rule, but exact observations are lacking.

Throughout the greater part of the year the individuals of this species are scattered out over the country. Each then occupies its own little individual shelter of the sort just indicated, and ventures forth at late dusk each night to hunt its food, returning at, or before, daybreak. The regular return to the same shelter observable in this species as with others of the genus indicates a strong 'homing' instinct.

The population of this species, in wild country and in farming districts, is often very large. The writer has had as many as five present in a town garden where the forage area was probably not more than 100 by 100 feet in extent. In cultivated fields, where the crops attract large numbers of insects which in turn are sought by toads, several individuals of the latter may be concentrated in a single day-time retreat; upon one occasion eight toads were found together in a small damp hole.

Halophilus is a heavy-bodied animal and does not travel rapidly either on land or in the water. The old adult females of large size

often walk instead of hopping, dragging the heavy hind limbs over the surface of the ground so that, on soft dust, the successive imprints of the hind feet, with five dots indicating the positions of the blunt-tipped toes, are connected by fine surface groovings in the dust. The rate of travel of an adult male was tested on one occasion, at night, on a lawn. The animal hopped (jumped) readily several times, but then settled down and walked, with rapid steps, moving one forefoot and the opposite hind foot in unison. After going about 15 feet the toad settled down and was reluctant to move farther. When in the water, *halophilus* swims either with the forelegs pressed along the sides of the body or else with the forefeet directed forward; in the latter case progress is slower.

Toads, because of their habit of living around human habitations, suffer accidents at the hand of man not experienced by other species of native amphibians. With the advent of automobile travel many of the animals are killed while attempting to cross well traveled roadways. Indeed, toads are becoming scarce in well settled communities, largely as a result of automobile travel. With horse-drawn vehicles the animals were usually able to escape disaster, but they cannot move quickly enough to avoid the motor vehicle. Furthermore, when strong headlights are suddenly flashed upon a toad, the animal usually stops motionless in the road and is crushed. During the spawning season numbers of large adults are killed each year while crossing roadways en route to ponds.

An unusually large number of mutilated toads was discovered on a golf course at Altadena, Los Angeles County, in 1923, when the writer visited some cement-lined reservoirs there on the night of April 8. Following rains during the preceding week, *halophilus* was out in numbers, on the lawns, around the margin of the pools, and in the shallow water along the 'shores.' There was a regular guard of toads spaced at intervals of from 10 to 15 feet around each pool. Upon picking up a number of these they were found to be males—awaiting the advent of females ready to spawn. Fully 50 per cent of these animals were found to possess mutilated limbs. The deficiencies ranged from the loss of a few toes to the loss of an entire hind foot and tibia up to the 'knee'; less often a fore limb was abbreviated. Only one member was affected on each of the toads seen. Several of the cut limbs had been sheared off slantingly in a manner which suggested that the damage had been done by a lawn mower. The golf greens are cut by engine-driven mowers which travel at a rate too rapid to permit of a toad getting out of the way. Some cripples were

seen in the pools in addition to those out on land. The animals in the water were obviously hampered in their swimming; instead of pursuing straight courses they often circled about.

Crosswhite and Wyman (1920, p. 78) have figured an adult of this toad (presumably from southern California) which had a supernumerary leg attached medially to the posterior end of the body. This limb bore two well-formed feet, reversed right for left. The possession of this abnormal development was evidently not a particular hindrance to the animal.

The breeding season of *halophilus* occupies a long period. In southern California, Camp (MS) says that it breeds from January to June. In the central part of the State the months of March, April, and May witness most of the spawning. At the higher altitudes in the mountains breeding is probably delayed until June or July, as with *canorus*. The following table gives all of the exact information which the writer has been able to gather upon the spawning activities of this species.

SPAWNING DATA FOR *Bufo boreas halophilus* IN CALIFORNIA

Locality	Date	Nature of material
Arroyo Seco, Los Angeles at Avenue 66	Jan. 28, 1923	Eggs (L. H. Miller, MS.)
Stockton, San Joaquin Co.	Mar. 12, 1923	Laying in progress; some young larvae
East Oakland, Alameda Co.	Mar. 15, 1914	Adults taken to laboratory laid during night
San Francisco Bay region	Mar. 28, 1920	Toads collected this date laid during night (P. E. Smith, MS.)
East of Buckman Springs, San Diego Co.	Mar. 29, 1923	Freshly laid eggs and early embryos
Sierra Madre, Los Angeles Co.	Apr. 4, 1923	Embryos and advanced larvae
Altadena, Los Angeles Co.	Apr. 8, 1923	Eggs nearly ready to hatch and others just laid
Arroyo Seco, Los Angeles	Apr. 15, 1923	Larvae 10 to 32 mm. long
Oakland, Alameda Co.	Apr. 16, 1912	Paired adults taken to laboratory spawned during night
Lafayette, Contra Costa Co.	Apr. 19, 1922	Laying in progress
4 miles west of Dixon, Solano Co.	May 1, 1924	Laying in progress
Lafayette, Contra Costa Co.	May 7, 1921	Larvae reported
Lafayette, Contra Costa Co.	May 14, 1921	Larvae of several sizes, some recently hatched
Davis, Yolo Co.	May 21, 1924	Large larvae and one transformed toad
Lafayette, Contra Costa Co.	May 22, 1921	One lot of freshly laid eggs
Manor, Marin Co.	July 6, 1919	Many young toads just transformed

Stejneger (1893, p. 220), under *Bufo halophilus*, records the finding of tadpoles on the East Fork of Kaweah River at an altitude of 10,200 feet on August 7, 1891. The same author lists numerous "adol." [adolescent = transforming?] individuals as follows:

Alvord, Owens Valley	4,000 feet	June 26, 1891
Lone Pine, Owens Valley	[3,700 feet]	June 6, 1891
Round Valley, Tulare Co.	10,000 feet	Aug. 22, 1891
Whitney Meadows	[9,800 feet]	Aug. 20, 1891
Kings River [Fresno Co.]	5,200 feet	Aug. 19, 1891
Elizabeth Lake, Los Angeles Co.	[3,400 feet]	July 2, 1891

When the adults of this species repair to the water for spawning they do not, so far as the writer is aware, ever congregate by "hundreds" or "thousands" as is occasionally reported to be the case with *americanus* of eastern America or *vulgaris* in western Europe. Ordinarily a dozen or fifteen pairs will constitute the breeding population of *halophilus* at any one spot. The males, while in the water, utter series of low mellow tremulous notes. In chorus the notes may be compared to the voicings of a brood of young domestic goslings. The call of each male is uttered for a second or two and repeated at short intervals so that a practically continuous chorus issues from a breeding colony. To human ears the notes lack carrying power and can scarcely be thought to be of use in attracting toads at any great distance from the pools where the males are calling. Occasionally males in their daytime retreats will utter the notes once or twice. This species does not have an enlarged vocal pouch such as is possessed by many species of toads (for example, *americanus, cognatus, woodhousii*), and this lack of a "resonating pouch" is probably responsible for the small volume of sound uttered. Calling, with *halophilus*, is to be heard in the daytime as well as at night.

The mating amplexion in this species is axillary, as described for other species of the Bufonidae.

As spawning places, *halophilus* uses the margins of permanent or temporary ponds, temporary roadside pools, cement water reservoirs, and the margins of flowing streams. Eggs are usually deposited in water 150 millimeters or less in depth. On one occasion, at Lafayette, toads were spawning at the surface of a flowing stream which was fully 300 millimeters in depth.

The egg complement of this species is very large. Many of the old adult females measuring 100 millimeters or more in head-and-body length contain enormous masses of eggs. Camp (MS) estimates the

egg complement of *halophilus* to be as much as 10,000. The present writer has measured the total spawn of one mated pair of toads from Lafayette which was isolated and which spawned in captivity on April 19, 1922. The total volume of the spawn was 325 cubic centimeters. A sample of 26.5 cubic centimeters contained 1351 eggs by actual count, so the total mass was calculated to contain about 16,500 eggs. These figures are much larger than those given by Wright (1914, p. 32) for *Bufo americanus* at Ithaca, New York.

The eggs of this species are deposited in long slender strings of jelly (pl. 14, fig. 43), circular in cross-section. These strands are extruded (in pairs) intermittently over a period of some hours (5 hours in the case of one captive pair, 8 hours with another), and when spawned in pools or creeks containing aquatic vegetation the movement of the toads here and there in the water while laying is in progress results in the egg strands being woven about the vegetation.

An individual egg string of *Bufo boreas halophilus* measures 4.89 to 5.29 millimeters in outside diameter. There is an outer cylindrical sheath, the walls of which are 1.35 to 1.45 millimeters in thickness. Within this is a cylindrical core 3.54 to 3.82 millimeters in diameter and in this the eggs are held, in two, occasionally three, lengthwise rows. Individual eggs measure 1.65 to 1.70 millimeters in diameter. The vitelline capsule is close about the egg, measuring only 1.70 to 1.75 millimeters in diameter (fig. X). The jelly, when freshly laid and swollen to normal size, is as clear as that on any of the eggs of the water-spawning amphibians of central California. I failed to find segmentation in the inner core such as is shown by Wright (1914, p. 17, fig. 1A) for *Bufo americanus*. The jelly in most natural locations usually soon becomes coated with fine sediment.

Embryonic development is rapid. One lot of eggs taken to the laboratory at Berkeley on April 15, 1912, was hatching on April 20. Another lot taken on April 19, 1922, kept in a small aquarium which received sun for only a portion of each day, hatched out about April 28. In the field, especially in the interior valleys and in southern California, hatching probably occurs in a shorter period.

At my request Mr. Philip N. Baxter kept track of the stock of *Bufo boreas halophilus* in a pool at Stockton, San Joaquin County, during the late spring of 1922. Collections were made at short intervals during April and May. The following table, based on this material, shows the increase in size in the general population with the advance of the season.

Date	Total length in millimeters	Remarks
April 19	9 to 24	
April 21	12 to 26	Specimens 18 mm. long with limb buds
April 24	13 to 37	
April 29	24 to 48	
May 1	12 to 37	Hind limb buds small on largest specimens
May 5	11 to 50	Mostly well above 11 mm., but some apparently only a day or two old
May 8	— to 42	
May 13	13 to 56	Mostly of large size
May 17	19 to 46	
May 22	19 to 52	Metamorphosis under way; one completely transformed toad

On cold or windy days the tadpoles in this pool would be gathered in the deeper waters of the pond, whereas on warm or hot days they were either distributed evenly throughout the water or else gathered in 'swarms' in the shallows close to the shore (pl. 14, fig. 44).

A batch of larvae collected in the Arroyo Seco at Avenue 66, Los Angeles, on April 15, 1923, ranged from 10 to 34 millimeters in total length. Well developed hind limbs were present on one which was only 27 millimeters in length.

The prolonged laying period results in the appearance of newly developed young toads through a long season in the late spring and summer months. Metamorphosis is accomplished by May in some hot interior localities, whereas in the coast region toad larvae are still to be seen in July.

For some time after metamorphosis the young toads frequent the damp shores of the ponds in which their larval development took place. The time at which general dispersal from the breeding places to the surrounding territory occurs has not been determined. The next known stage, found here and there over the country, in the winter season, is the young animal about 30 millimeters in head-and-body length.

Growth to sexual maturity, as indicated by the size (age) groups encountered in general collecting, requires at least two full years. I am uncertain as to whether or not the animals first breed at two or at three years of age.

The life-history in relation to the environment.—This toad is the only member of its genus and family throughout the greater part of its range. It occurs over a wide expanse of territory in which great

differences are experienced in the environmental factors of temperature, relative humidity, evaporation ratio, and percentage of sunshine. At the lower altitudes *halophilus* seems to be active throughout the year. Being terrestrial in habit, it does not have the moist environment enjoyed by the ranas nor does it possess, like *Scaphiopus*, digging equipment which would enable it to burrow deeply into the ground during the dry season. *Halophilus* uses any sort of available cover which will give it shelter against desiccation. By reason of its large supply of dermal poison glands it experiences relative freedom from enemies among carnivorous birds and mammals; at least there are very few reports of the finding of remains of this species in the stomachs of such predators. Lacking other protection than that just indicated, the large size of the adults seems to be an indication of the efficacy of this sort of protection. Food is fairly abundant in the form of terrestrial insects, especially nocturnally active species likely to escape the attention of diurnal insectivorous birds. The toad, by virtue of its lesser rate of metabolism associated with non-regulated body temperature, is probably better able to fast during times of food shortage than insectivorous birds or mammals under similar circumstances.

The nocturnal habit of the toad is an important factor so far as avoidance of desiccation is concerned. In the humid coast belt there is always a high degree of atmospheric humidity day and night and therefore little danger from desiccation. In interior localities of California where the midday temperature is high, there is almost always a sharp drop in temperature after sunset. This raises the relative humidity of the air. The colder air, being heavier, tends to sink to the surface of the ground so that the layer of air immediately above the ground has the greatest relative humidity. The toad's activities are adjusted to this daily fluctuation. Rapid desiccation and death of the adult would be apt to follow indulgence in daytime foraging.

At the spawning season the adults betake themselves to pools of water. There the moisture ratio at and just above the water surface is high enough to protect the animals against injury by desiccation. Ellis and Henderson (1915, pp. 254–255) report the finding in Colorado, of large numbers of young *Bufo boreas* in water about an overflow pool of a hot spring at 23° C. Toads were abundant up to where the water was 34° C. (93° F.) and one live individual was observed in water at 45° C. The animals are evidently able to withstand relatively high temperatures if there is adequate moisture.

The spawning season of the toad is late as compared with that of other water-spawning amphibians. Typically the toad lives in situations apart from permanent bodies of water and spawns chiefly in temporary pools. During the earlier part of the year (January to March) these are as cold or colder than the surrounding air. Deposition of eggs in such locations would result in slow development at best. The growth of algae in such pools is slow. After the advent of warm weather algae increase rapidly and this affords abundant food for the larval toads. Furthermore, the increase in water temperature results in an increase in the body temperature of the larvae (which are practically black in color, a feature which makes for the greatest possible absorption of heat rays from the sunshine). There is a marked tendency for toad larvae to gather in the shallowest marginal portions of the pools, where their bodies are just barely covered by the water, where the water and even the mud bottom beneath the water are materially warmed by the sun, so that the animals get the greatest possible benefit from the heat (pl. 14, figs. 43, 44). The well-known law of Van't Hoff and Arrhenius applies (within certain limits) to the growth processes of living organisms. Hence in the case of the toad, delay in spawning until the advent of warm weather results in the speeding up of the rate of development and a shortening of the total time in the egg and larval stages. The species therefore passes through this most critical aquatic period in the least possible time, a matter of great importance late in the season when pools are apt to dry up rapidly.

At emergence the young toad is of very small size, only slightly larger in actual size than the young tree-toad; relative to the size of the adult it is far the smallest of any of our amphibians. This small size is related to several factors. The delay of the spawning period until late in the season greatly increases the risk that one or all of the eggs laid by any one pair of toads will not survive the aquatic stage. To compensate for this the egg complement is found to be large. For *Bufo. b. halophilus* it is the largest of any of the native central California amphibians. Small size of egg and resulting larva is also related to rate of development. The total bulk of nutriment required for the aquatic larva is lessened by the small size of the tadpole. Small size upon transformation to the adult condition is of advantage in enabling the young toad to take shelter in very small crevices, insect burrows in the ground beneath rocks, and in other similar places. The greatest danger immediately subsequent to metamor-

phosis in the case of the toad is neither food nor enemies but desiccation. The high temperature conditions obtaining in early summer would quickly dry up either a small toad or a large one. But the small individual stands a greater chance of finding shelter than the large one.

Following metamorphosis, at least two years elapse before the toad arrives at sexual maturity. This delay is probably to permit the adult, particularly the female, to acquire a certain minimum size before undertaking the task of egg production.

Bufo canorus Camp. Yosemite Park Toad

(Pl. 17, fig. 51; text figs. MM, OO)

Bufo canorus Camp (1916*c*, pp. 59–62, text figs. 1–4). Original description, type from Porcupine Flat, 8100 feet, Yosemite National Park, California.

Bufo canorus, Grinnell and Camp (1917, pp. 143–144, fig. 4). Range.

Bufo canorus, Stejneger and Barbour (1917, p. 27; 1923, p. 24). Range.

Bufo canorus, Grinnell and Storer (1921, p. 178). Occurrence.

Bufo canorus, Grinnell and Storer (1924, pp. 657–660, pl. 60*d*, *e*). General account of discovery, habits, and life-history.

Diagnosis.—Size small, head-and-body length up to 71 millimeters (2¾ inches); parotoid glands broad, breadth equal to length of orbit, space between glands scarcely more than width of one gland; no cranial crests; dorsal coloration of males chiefly olive green, of females brown with large white-rimmed spots of black.

Comparisons.—Distinguished from other California Salientia except Bufonidae by presence of enlarged parotoid glands on shoulder region; from *Bufo alvarius, cognatus,* and *woodhousii* by absence of cranial crests, from *Bufo punctatus* and *Bufo boreas* ssp. by narrow space between parotoid glands (less than width of one gland).

Description.—Form moderate, depressed, limbs short; head oval in outline from above, thick in profile; muzzle descending, steep-fronted; external nares nearly terminal, on slightly raised bosses, directed anteriorly; canthus rostralis distinct, about two-thirds as long as orbit; orbit large; interorbital space less than half length of orbit (slight indication of cranial crests on some males); tympanic membrane small, slightly higher than wide, anterior margin below posterior portion of orbit; parotoid glands relatively large, flat, subcircular, separated by space not greater than width of one gland; outline of lower jaw semicircular (male) or acutely oval (female); angle of jaw under posterior margin of orbit; no gular fold; fore limb short, much stouter in male than female; about half of upper arm included in skin of body; forearm usually longer than hand; one large broad tubercle on center of palm, another much smaller tubercle at base of first finger (female) or two subequal palmar tubercles (male); fingers moderate,

innermost stoutest, in order of decreasing length, 3, 4, 2, 1; body longer than broad, depressed; hind limb more slender than fore limb; half of femur free from body skin; tibia shorter than femur; tarsus about three-fifths length of tibia, and about one-third length of whole foot; two metatarsal tubercles, inner much better developed than outer; toes slender, small, in order of decreasing length, 4, 3, 5, 2, 1; web restricted, along sides of toes to ends but deeply notched.

Tongue oblong, rounded at both ends, width less than half that of mouth at angle of jaws, attached broadly for anterior half to floor of mouth; internal nares rounded, far forward in roof of mouth.

Surfaces generally smooth, warts low, flattened and rounded; ventral surface irregularly areolate, rugose posteriorly, especially on ventral surface of femur; palm with few low rounded tubercles of small size; sole smooth with sesamoid tubercles imperfectly indicated.

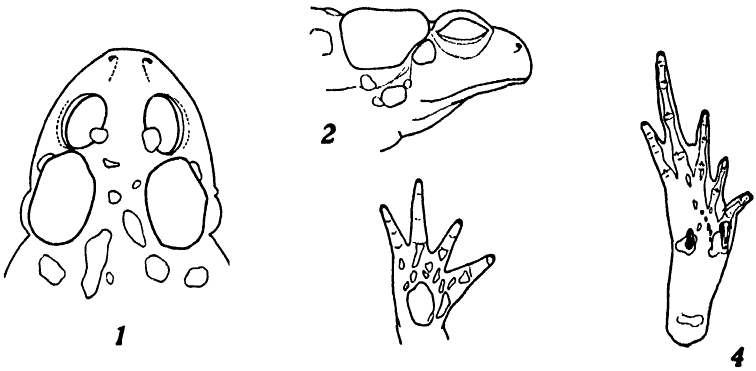


Fig. OO. *Bufo canorus*, female (no. 5744, M. V. Z., type), natural size (after Camp, 1916*c*, p. 60).

1. Top of head, showing width of parotoid glands and relatively narrow interspace and shape of snout.
2. Lateral view of head, showing extent of parotoids and steep profile of snout.
3. Right front foot, plantar surface.
4. Right hind foot, plantar surface, showing slender outline and reduced webbing.

Color of female: All dorsal and lateral surfaces thickly marked with irregular but sharply defined patches of black, rimmed with white; dark patches reaching, but seldom crossing, midvertebral line; large warts in centers of dark patches, each topped with brown; ground color between dark patches, brownish white dorsally, clear white ventrally where marked with few scattered dark speckles.

Color of male: Upper and lateral surfaces of body olive green, flecked evenly and thickly with minute spots of black, each narrowly and evenly outlined with white; underparts dull white, with few spots, larger than those on back, of black.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo canorus* FROM YOSEMITE NATIONAL PARK, CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
5754	♀	Lyell Cañon, 11,000 ft.	July 16, 1915	59 0	16.0	21.3	8 0	3 0	15.0	15 0	21 0	20 4	12.0	36
5744[1]	♀	Porcupine Flat, 8100 ft..	July 1, 1915	68 1	17 5	25 4	8 2	3 7	15.8	17 0	26.7	24.0	14.5	40
5736	♀	Porcupine Flat, 8100 ft.....	July 1, 1915	69.5	19 0	23 7	7 5	3.8	17.0	18 0	28.0	23 8	14.7	40
7185	♀	Tamarack Flat, 6700 ft... .	May 25, 1919	69 5	19.0	24.0	8 0	2 5	17.2	13 4	26.0	24 8	15.0	40
5759	♀	1 mi. e. Porcupine Flat, 8100 ft. .	June 28, 1915	71 0	18 0	26 5	8.0	.	20 0	17.0	27 0	24 0	16.4	44
5760	♂	Lyell Cañon, 11,000 ft..	July 16, 1915	51 4	14 5	18 6	7 5	3 1	15 0	12.8	19 6	19.0	12.5	34
5726	♂	So. side Ragged Peak, 10,000 ft. . . .	July 9, 1915	52 3	15 0	19.0	7 2	3.7	13.7	13.1	19 4	19 0	12.3	33
5750	♂	Lyell Cañon, 11,000 ft....	July 16, 1915	53.6	15 3	20.0	6 7	4 3	14 0	14.0	23 5	19 9	13.0	37
5748	♂	Lyell Cañon, 11,000 ft. ..	July 16, 1915	55.0	16 0	20 4	8 0	3 4	15.4	12 3	22 0	19.8	13.0	37
5737	♂	1 mi. w. Ragged Peak, 9700 ft.	July 8, 1915	59 0	15 4	20 3	7 5	3 4	15 2	13.6	22 5	20 7	13.0	36

[1] Type.

Remarks on sexual dimorphism.—Sexual dimorphism and dichromatism is more marked in this species than in any other California salientian. The male, besides being smaller than the female, has fewer and smaller warts, the parotoid glands are reduced, and the body coloration is plain olive green marked with small scattered dots of black each rimmed with white. The female has low rounded warts of larger size than those in the male, her body coloration is brownish but this is largely obscured by the large white-rimmed black patches which mark the location of the warts. This dichromatism prevails at least from May until September, and presumably continues throughout the year.

Range.—This distinct species, discovered in 1915, is confined to the higher altitudes (above 6500 feet) in the central Sierra Nevada of California. All the stations of record to date are in Yosemite National Park. On the west *canorus* has been collected at Tamarack Flat, altitude 6700 feet, on the Big Oak Flat Road, and near Peregoy Meadow, 7500 feet, on the road between Chinquapin and Glacier Point. The easternmost locality of record is Tioga Lake, 10,000 feet; the highest station is in the head of Lyell Cañon at 11,000 feet. The life-zones represented are Canadian and Hudsonian. The territory north and south of the Yosemite region has not been explored sufficiently to prove whether *canorus* occurs beyond the Park boundaries. At Lake Tahoe *Bufo boreas boreas* is found; in the vicinity of Mount Whitney

Bufo boreas halophilus is the only toad which has been collected. The former subspecies occurs about Mono Lake just a few miles east of the easternmost record station for *canorus,* but in a lower life-zone; *Bufo b. halophilus* occurs on the western flank of the Sierras, but again in lower zones (Upper Sonoran and Transition). In the eastward penetration of the Transition Zone on the floor of Yosemite Valley *halophilus* actually occurs east of the westernmost stations of occurrence for *canorus,* but the difference in altitude is fully 2500 feet.

Life-history.—*Bufo canorus* is strictly a high mountain toad. Its life-history has not been completely investigated although a number of facts concerning it were learned by members of the field parties of the Museum of Vertebrate Zoology when working in the Yosemite National Park in 1915 and 1919. The following is an abridgement of the account given by Grinnell and Storer (1924, pp. 657–660), which includes most of the known facts. All observations were made in Yosemite National Park.

Bufo canorus undoubtedly hibernates for a considerable period of time during the winter months, when snow covers the higher country and the air temperature goes below the freezing point; in this respect it differs markedly from the majority of amphibians in California. Observations were not continued within the range of the species long enough to determine the actual dates of spring emergence and fall disappearance. On May 20, 1919, at Peregoy Meadow, south of Yosemite Valley, males were already out and trilling loudly, and on September 3, 1915, at Vogelsang Lake, a single individual was collected. Some of the toads probably emerge toward the end of April and a few may be out until early October. The hardihood of the species is indicated by the way in which the adults enter the melting snow water during the spring and early summer months. The winter season is spent in some retreat in the ground, presumably below the frost line. During that part of the summer not devoted to spawning activities the toads spend the days solitarily in damp situations at the surface of the ground under logs or stones. Several small individuals were observed in the daytime in July on a hot, dry, sandy flat near Ragged Peak, and near Vogelsang Lake one individual was found beneath a rock in a damp heather patch 20 feet from a stream.

Immediately or very soon after emerging from their winter hibernation these toads repair to pools and small streams in the wet meadows, and continue there until the eggs are deposited or even longer. The males precede the females, as

at Peregoy Meadow there were many males present on May 20, 1919, while the only females found were small non-breeding individuals. At Tamarack Flat, May 25, 1919, an adult female was found at the base of a rotted tree stump fully 200 yards from the edge of the nearest meadow and 200 feet above it in altitude, while males were heard trilling in the meadow that same evening. On June 15, 1915, a chorus of these toads was heard near Peregoy Meadow, although egg laying had been accomplished some time previously. At Snow Flat on June 28, 1915, and near Ragged Peak on July 9, 1915, other toads were heard in song. At the head of Lyell Cañon on July 16, 1915, numbers of Yosemite Toads were found in a small pond, and at least some of the females were engaged in laying their eggs.

On May 20, 1919, numbers of male Yosemite Toads were congregated in the wet meadows on either side of the ridge east of Chinquapin. During the preceding winter gophers from the adjacent slopes had moved down and occupied the grassy meadows, but with the spring break-up and melting of the snow the place had become untenable for the gophers, who had moved up onto the hillsides once more. Their tunnel systems were left as subterranean 'pipes' which carried off much of the water from the melting snow banks to the creek in the bottom of the cañon. These gopher tunnels served also as shelters for the toads. The latter when partially hidden in the entrances to the tunnels or even when they sat quietly on the open grassland were quite invisible to our [human] eyes, so well did their pattern of coloration match the greens and browns of the meadow.

The mating song of the Yosemite Toad is a sustained series of ten to twenty or more rapidly uttered notes, constituting a 'trill,' and the whole song is repeated at frequent intervals. The notes, though mellow in character, carry well considering the size of the animal and have a ventriloquial quality which makes it difficult to locate any one animal by sound alone. When a number of males are giving their songs in the same place the songs overlap one another so that the general chorus is continuous. There is some difference in the pitch at which the several members of a group sing, varying perhaps with the size of the individual toad. Singing is carried on through the daylight hours and into early evening at least. . . .

The Yosemite Toad spawns in late spring or in summer, depending somewhat upon the local climate. Specimens collected on May 24 to 26, 1919, at Tamarack Flat showed no signs of breeding. On June 22, 1915, numerous tadpoles and one recently metamorphosed young toad were seen at Mono Meadow. One female taken near Porcupine Flat June 28, 1915, had already laid most of her eggs. On July 16, 1915, at the head of Lyell Cañon several individuals were depositing eggs. [On a visit to Mount Dana on July 22, 1921, Mr. Stanley B. Freeborn found well developed larvae in some ponds at timber line, altitude 10,500 feet (Storer, MS).]

The collection of Yosemite Toads at hand includes 20 males and 28 females. The size-groups indicate that about four years are required for a toad to reach adult size, that males are always somewhat smaller than females of the same age, and that the females do not begin to spawn until more than 50 millimeters in length, when they are presumably three years old.

Among the females taken are three which measure 20, 22, and 23 millimeters in length; these are 'yearlings.' Another group of 12 ranging from 33 to 49 millimeters represents the 'two-year-olds.' In

neither of these two size-groups did any of the individuals show that eggs were being, or had been, developed. The third group, of 9 animals, measures about 57 to 62 millimeters in length; and the fourth of 4 individuals about 70 to 74 millimeters. In both the latter groups the animals were in breeding condition and contained eggs.

Male toads in the collection fall into two groups: 50 to 55 millimeters, and 58 to 64 millimeters in length. These specimens were practically all collected in meadow ponds or streams and were breeding animals, for they have nuptial excrescences on the inner digits of the fore limbs. They are believed to represent animals three and four (or more) years of age. No males were obtained which could be called younger than these. Such individuals would probably be found by careful search on the upper slopes some distance from the breeding ponds.

"The food of the Yosemite Toad includes a wide variety of insects and the like. One individual captured at Porcupine Flat, June 29, 1915, contained two Tenebrionid beetles, several weevils of different species, numerous large ants, and one centipede, besides some red fir needles probably taken incidentally." (Quoted items from Grinnell and Storer, *loc. cit.*)

Bufo cognatus cognatus Say. Great Plains Toad

(Pl. 11, fig. 31*a*)

Bufo cognatus Say *in* Long (1823, vol. 2, p. 190, footnote). Original description, type from Arkansas River [in Colorado, probably between present site of La Junta and Colorado-Kansas boundary: see Grinnell and Camp, 1917, p. 140].

Bufo cognatus, Cope (1889, pp. 275–277, fig. 67). General account.

Bufo cognatus, Dickerson (1906, pp. 99–102, col. pl. 5 [fig. 2], pls. 30 [figs. 85–87], 31 [figs. 88–89], 32 [figs. 90–92], 34 [figs. 99–100]). General account.

Bufo cognatus cognatus, Camp (1915, pp. 327, 331). Along Colorado River and in Salton Sea basin; critical.

Bufo cognatus cognatus, Grinnell and Camp (1917, pp. 140–141, fig. 4). Range in California.

Bufo cognatus cognatus, Stejneger and Barbour (1917, pp. 27–28; 1923, pp. 24–25). General range.

***Diagnosis*.—Size moderate, head-and-body length up to 80.3 millimeters (3¼ inches); cranial crests well developed, diverging posteriorly, joined anteriorly by a raised boss on muzzle; parotoid glands short and broad, scarcely longer than orbit; inner metatarsal tubercle with large dark-colored, free cutting edge; vocal sac of male bladder-like, emerging at middle of throat on line between bases of fore limbs.**

Comparisons.—Distinguished from all other California Salientia by combination of divergent cranial crests, short widely separated parotoid glands, and narrow-edged inner metatarsal tubercle; from *Scaphiopus hammondii* by horizontally instead of vertically elliptical pupil, roughened dorsal surface, and presence of conspicuous parotoid glands and cranial crests; from *Bufo alvarius, Bufo boreas* ssp., *Bufo canorus,* and *Bufo punctatus,* by presence of angular cranial crests together with conical warts; from *Bufo woodhousii* by greater angle between cranial crests, by presence of raised boss joining crests on muzzle, by shorter, more oval, and relatively higher parotoid glands, by smaller warts on dorsal surface, shorter hind foot, and by restriction of vocal sac to midpart of lower throat region (compare pl. 11, figs. 31*a*, 31*b*); from *Bufo cognatus californicus* by presence of external cutting tubercle on hind foot, and by lack of large green spots on dorsal surface.

Description.—General form stocky; head thick in profile, greatest thickness about two-thirds its own length; outline of head from above acuminate oval; muzzle short, less than length of orbit, slanting in profile, rounded at tip; external nares at tip of muzzle, opening anteriorly; canthus rostralis not always developed; orbit proportionately large, half length of head; interorbital region moderate, somewhat concave; cranial crests well developed, closely approximated anteriorly where joined to distinct raised nasal boss, thicker and widely divergent posteriorly; preorbital crest slight; postorbital crest conspicuous, meeting longitudinal segment of crest at an obtuse angle, and extending laterally to above tympanic membrane; tympanic membrane vertically oval, longer axis about half length of orbit, sometimes overhung by margin of parotoid gland; parotoids short, oval, length about one and one-half times that of orbit, slightly divergent posteriorly, in contact with transverse segment of cranial crest anteriorly; lower jaw oval in outline; vocal sac of male not occupying chin but emerging as a bladder-like structure centrally at base of throat; body evenly rounded, nearly as wide as long; fore limb moderate, fully half of upper arm included in body skin; forearm slightly longer than hand; hand stout; one large flat palmar tubercle; fingers short, in order of decreasing length, 3, 1, 2, 4; first finger stoutest; ventral surface of fingers with many small tubercles; most of femur buried in body skin; tibia slightly shorter than femur; tarsus about two-fifths length of foot; two conspicuous dark-edged metatarsal tubercles, inner one much larger and with free cutting edge; toes small, in order of decreasing length, 4, 3, 5, 2, 1; plantar surface of foot much smoother than that of hand.

Tongue ovate, small end forward, width about half that of mouth at angle of jaws, attached by anterior half to floor of mouth; internal nares small, pyriform, far forward in mouth.

Nasal boss and upper labial region smooth; parotoid glands smooth; eyelids and dorsal and lateral surfaces of body and exposed surfaces of hind limbs, covered with many closely placed rather sharp-pointed warts less than 2 mm. in diameter at base; warts on fore limb smaller and lower; ventral surface of body irregularly areolate.

General coloration light or dark yellow or gray; narrow vertebral stripe white or pale yellow; dorsal surface with large irregular-margined dark spots roughly in bilateral series as follows: on eyelid, inside and outside of parotoid gland, just posterior to parotoid, middle of back (several) and on rump; spots blackish in preserved specimens, greenish in life; ventral surface of body and limbs, dull yellow; vocal sac of males bluish black; limbs irregularly cross-barred with black; tips of all digits and metatarsal tubercles, brownish black.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo cognatus cognatus* FROM SOUTHEASTERN CALIFORNIA

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4357[1]	♀	July 16, 1909	66.0	19.6	25.3	9.8	4.0	17.5	16.0	25.0	24.5	15.5	41
1133[1]	♀	July 16, 1909	67.2	19.7	27.4	10.0	4.0	17.6	15.9	26.8	23.7	15.0	39
4356[1]	♀	July 16, 1909	69.0	19.7	27.0	9.0	3.5	17.3	15.5	27.2	24.6	14.0	40
1059[2]	♀	May 4, 1909	73.0	20.5	28.5	10.0	3.7	18.1	18.3	28.8	25.3	16.2	41
464[3]	♀	Apr. 20, 1908	80.5	21.8	29.0	10.0	3.5	19.0	17.9	34.6	26.5	17.0	48
465[3]	♂	Apr. 28, 1908	56.2	17.0	21.0	8.4	2.8	14.0	13.9	23.0	20.3	13.3	35
462[3]	♂	Apr. 21, 1908	58.3	17.0	21.2	8.8	3.0	16.2	14.4	21.3	20.7	13.0	35
1139[1]	♂	July 16, 1909	60.0	18.0	28.7	8.3	3.0	16.0	14.6	26.8	23.0	14.3	38
1134[1]	♂	July 16, 1909	63.7	19.3	24.3	8.2	3.0	16.4	13.7	28.9	23.3	15.1	35
1138[1]	♂	July 16, 1909	66.0	19.7	24.3	10.0	3.3	16.8	15.4	28.3	26.0	15.5	39

[1] Needles, San Bernardino Co.
[2] Brawley, Imperial Co.
[3] Mecca, Riverside Co.

History.—This was the earliest western amphibian to be described, as the first specimen, obtained in 1819 or 1820 by Long's expedition to the Rocky Mountains (probably in eastern Colorado), was described by Say in the report of that expedition in 1823. Cope in 1879 described an apparently abnormal individual, lacking cranial crests, as *Bufo dipternus,* but he later relegated the name to synonymy. *Cognatus* has in the past occasionally been listed as a subspecies of the wide-ranging *lentiginosus* (=*americanus*), but it is quite distinct from that species. The *cognatus* population in California west of the desert was separated by Camp in 1915 as a distinct subspecies, *californicus.*

Range.—*Bufo cognatus cognatus* occupies a wide extent of territory including the Great Plains and the southern part of the desert area along the Mexican boundary west to California.

Cope (1879, p. 437), in the description of his *Bufo dipternus,* gives the locality of capture of the type as "plains north of the Missouri River east of Fort Benton" [=Montana]. If this material is properly referable to *cognatus* then the range of the latter is carried nearly to the Canadian boundary. The same author (Cope, 1889, p. 277) states that he obtained additional specimens near the Judith River, which empties into the Missouri about fifty miles east of Fort Benton. Cary (1917, p. 27) lists this species from the Upper Sonoran Zone in Wyoming, without locality. It is said to occur in the Dakotas, but I can find no definite records. In Nebraska the species has been found at Fort Kearney and "Fort Pierre," in Kansas at Fort Riley, and in Arkansas on the Red River and "Pale Creek" (Yarrow, 1883, p. 165). In Colorado, Ellis and Henderson (1913, p. 56) say that it is a "plains species, coming into the foothills region." According to their records it skirts the eastern base of the Rockies from Julesburg and Greeley on the north to Costello County at the south. It has been found at Fort Garland (Yarrow, 1875, p. 521). Dickerson (1906, pl. 32 [figs. 90, 92]) indicates Denver as a locality of record; the color pattern of the specimens shown in the figures is different from that of *cognatus* to the south and west. In Texas this species occupies only the extreme western part, in the "Panhandle" district, as on the headwaters of the Brazos River (Cope, 1892, p. 332), at Goodnight, Armstrong County, about El Paso (Strecker, 1915, p. 52), and at Sierra Blanca, El Paso County (Bradley, 1919, p. 413).

In New Mexico this species has been recorded at Albuquerque (Van Denburgh, 1924, p. 196). The same author mentions a specimen in the U. S. National Museum from near Monument 66 on the Mexican boundary. Camp (1915, p. 333) lists a specimen from the same collection (no. 21065) with the following data: "Animas Valley (Colorado?) September 9, 1895?" Accompanying this is a toad of the same species (no. 21070) from Fort Huachucha, Arizona, taken in July, 1893. A study of the diary of Major E. A. Mearns (1907, pp. 14, 15, 92) convinces me that the Monument 66 and Animas Valley records are based on one specimen and that the animal in question was collected by Mearns on the eastern margin of Las Animas Valley, Grant County, New Mexico, on September 9, 1893. Mearns was at Fort Huachucha, Arizona, July 17 to 27, 1893. The record given by Yarrow (1875, p. 521) and repeated by Cope (1889, p. 267) for "Ralston, Ariz." probably relates to a place of this name in extreme southwestern New Mexico, in the vicinity of the present town of Lordsburg.

A map in the volume containing Yarrow and Henshaw's 1878 paper shows this town.

In Arizona *cognatus* has been found at Tucson (Stone, 1911, p. 223) and Camp Crittenden, Pima County (Yarrow, 1875, p. 521), at Phoenix, Maricopa County (Dickerson, 1906, pl. 31), and at Yuma (Van Denburgh and Slevin, 1913, p. 395). In old Mexico it has been reported from Coahuila (Yarrow, 1883, p. 165). In California this toad lives along the Colorado River from Fort Yuma to Needles (Mus. Vert. Zool.), and in the Salton Sea region at Mecca (Grinnell and Camp, 1917, p. 141), and at Brawley (Mus. Vert. Zool.). The California Academy of Sciences has specimens from Blythe and Coachella. *Cognatus* seems not to have been found in the Great Basin; at least no records are at hand from either Nevada or Utah.

Life-history.—Practically nothing is on record concerning the life-history of this species. Dickerson (1906, pp. 93, 101) says of specimens in captivity that the voice of *cognatus* is decidedly unmusical.

> The male . . . 'talks' in a voice resembling the squawk of a toy doll. This squawk of the *Bufo cognatus* is much like the sound produced by *Bufo halophilus* of California. The harsh note is given over and over again at brief intervals until the cause of the annoyance is removed. The pitch of the note is low, ranging from B to A below middle C. In the midst of the harsh low-pitched notes, the toad sometimes surprises one by giving a cry pitched about two octaves above (usually A).

As shown in a photograph (Dickerson, 1906, fig. 100) the peculiar vocal pouch of *Bufo cognatus* can be distended to tremendous size, equaling a third the bulk of the body.

The collection of *cognatus* at hand includes 25 specimens from southeastern California. Of these one (no. 4354, Mus. Vert. Zool.) taken July 13, 1909, measures only 17.5 millimeters in head-and-body length; it is obviously of the year's brood and but recently metamorphosed. A second size-group includes individuals from 27.8 to 41.0 millimeters in length; these I take to be 'yearlings.' A third category ranges from 47.6 to 73 millimeters, while there is one measuring 80.5 millimeters. Thus four years, at least, seem to be required to attain full size. The third category probably includes two age-groups. Dickerson (1906, p. 101) says that "judging from the series of decidedly different sizes of this toad found in the spring, at least five years must be required for full growth to be attained." There may be a size-group above that represented in the California material, as Ellis and Henderson (1913, p. 56) list two specimens from Jules-

berg and Wray, Colorado, each 100 millimeters in length. Camp's (1915, p. 333) "Animas Valley" specimen measured 89.8 millimeters in length.

Bufo cognatus californicus Camp. Arroyo Toad

Bufo cognatus californicus Camp (1915, pp. 331–333). Original description, type from Santa Paula, Ventura County, California.
Bufo cognatus californicus, Grinnell and Camp (1917, pp. 141–142, fig. 4). Range.
Bufo cognatus californicus, Stejneger and Barbour (1917, p. 28; 1923, p. 25). Range.

Diagnosis.—As for *Bufo cognatus cognatus* (which see), but external metatarsal tubercle absent, hind foot slightly longer, cranial crests somewhat (10 to 20 per cent) wider, and dorsal coloration uniform, without large spots of green.

Comparisons.—See *Bufo cognatus cognatus.*

Measurements.—No. 4364, Mus. Vert. Zool. (type), ♀, Santa Paula, Ventura Co., May 22, 1912: head-and-body length 63.6 millimeters; length of head 17.7; width of head 25.0; orbit 8.5; interorbital space 4.6; forearm 16.6; hand 16.0; femur 25.7; tibia 24.6; tarsus 15.0; whole foot 43.0.

Range.—Only two specimens of this toad have been taken to date. One was taken in Tujunga Wash near Sunland, Los Angeles County, on April 1, 1904. The second (type) specimen was taken at Santa Paula as above. Camp (1915, p. 332) says:

The type was found on a lawn in the middle of town, about eight o'clock in the evening. The Santa Paula district is about sixty miles east [actually about forty miles west] of the San Fernando Valley (where the other specimen of this subspecies was found), and a mountain spur about one thousand feet in elevation separates the two localities of capture. Both localities lie within the San Diegan faunal area in the Lower Sonoran life-zone, as the latter has been delimited in California. Both localities are of semi-arid character, and the streams are intermittent in the arroyos near which each of these toads was captured.

Bufo punctatus Baird and Girard. Spotted Toad

(Text fig. JJ)

Bufo punctatus Baird and Girard (1852*a*, p. 173). Original description, type from Rio San Pedro of the Rio Grande del Norte [= Texas].
Bufo punctatus, Yarrow (1883, pp. 22, 162). General range.
Bufo punctatus, Cope (1889, pp. 262–264, text fig. 60). General account.
Bufo punctatus, Stejneger (1893, p. 219). In Death Valley and Panamint Mountains, California.
Bufo punctatus, Dickerson (1906, pp. 110–112, col. pl. 5 [fig. 1], pl. 40 [figs. 116–120]). General account.
Bufo punctatus, Ruthven (1907, p. 507).

Bufo punctatus, Camp (1916*a*, pp. 509, 512). Description of larva; habits.
Bufo punctatus, Grinnell and Camp (1917, p. 144, fig. 4). Range in California.
Bufo punctatus, Stejneger and Barbour (1917, p. 29; 1923, p. 26). General range.

Diagnosis.—Size small, smallest *Bufo* in California, head-and-body length less than 75 millimeters (3 inches); parotoid glands short, rounded, placed low on shoulder region; cranial crests inconspicuous or lacking; eyes widely separated; warts very small, low and scattered, red-tipped in life.

Comparisons.—Distinguished from other California Salientia except Bufonidae by presence of small but distinct parotoid gland on shoulder region; from other California Bufonidae in general by very small low warts; from *Bufo alvarius* by small size, straight instead of curved cranial crests, and presence of reddish tips on warts.

Description.—General size small; head and body depressed; limbs relatively slender; whole head including muzzle flat-surfaced above; head truncately triangular as viewed from above, thin in profile; tip of muzzle at nares overhanging lower jaw; canthus rostralis distinct; external nares opening dorsolaterally below canthus rostralis; side of head below canthus and orbit steep; orbit large, its length nearly one-half length of head, margin of orbit projecting slightly beyond jaw; eyes widely separated, interorbital space about two-thirds length of orbit; cranial crests small, varying from slight lines of granules to distinct low ridges, but scarcely in evidence on living animal; each crest composed of straight longitudinal ridge along inner border of orbit joined to short transverse ridge extending between orbit and parotoid gland to above tympanum; tympanic membrane oval or nearly round, vertical diameter about one-half length of orbit; parotoid gland short, rounded or triangular in outline, of moderate height and smooth-surfaced, anterior border over middle of tympanic membrane; upper arm not deeply embedded in skin of body; forearm nearly equal to hand in length; two metacarpal tubercles, one opposite fourth finger, the other opposite first; numerous smaller tubercles on plantar surface of digits; digits slender except first, in order of decreasing length, 3, 1, 4, 2; dorsal surface of body evenly rounded; more than half of femur free from skin of body; femur usually slightly longer than tibia; tarsus about two-thirds length of tibia; foot slender; two small metatarsal tubercles opposite first and fifth toes; toes in order of decreasing length, 4, 3, 5, 2, 1; web deeply incised, only half of the one (basal) phalanx of fourth toe included; outline of lower jaw acutely oval.

Tongue narrow, less than half width of mouth at angles of jaws, oval in outline, attached along anterior two-thirds; internal nares large, placed far forward in mouth.

Labial region with enlarged warts; eyelids warty, interorbital region smooth; tympanic membrane smooth; parotoid glands covered with papillae; warts on dorsal and lateral surfaces of body small, low, and scattered; warts on lateral surface of head below tympanic membrane and on exposed surfaces of limbs more closely spaced than on body.

General color (in alcohol) of upper surface of body light or dark gray or brown; dorsal papillae orange or yellowish, larger ones encircled by black; under surface of body and concealed portions of limbs light yellow; limbs barred obscurely with black.

Stejneger (1890, p. 117) gives the following color description of a living specimen collected at the bottom of the Grand Cañon, Arizona:

Above "malachite-green" densely speckled with small dots of bright vermilion; limbs paler, dotted with vermilion and also with minute black specks which likewise occur on the flanks; region surrounding nostrils black; upper lips and whole under surface bluish-white, irregularly speckled with black; posterior part of belly and underside of thighs dark brownish flesh-color; soles, dull orange.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo punctatus* FROM CALIFORNIA

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
1081[1]	♀	May 26, 1909	51.4	14.8	19.2	7.0	4.2	12.1	12.6	19.6	19.4	11.8	29
1082[1]	♀	May 26, 1909	52.0	13.7	20.4	6.0	5.0	11.6	12.4	18.9	18.1	11.6	30
1086[1]	♀	May 26, 1909	52.0	14.6	20.2	6.8	4.6	13.4	12.2	20.9	18.9	12.1	30
6351[2]	♀	Apr. 7, 1917	55.5	16.2	21.3	7.3	5.3	14.0	12.5	21.7	21.3	12.6	34
6372[2]	♀	Apr. 8, 1917	57.0	15.6	23.0	7.3	5.6	13.8	12.8	20.6	20.6	11.7	31
1088[1]	♂	May 26, 1909	43.9	12.4	15.8	5.6	4.0	11.9	10.7	18.9	16.8	9.6	26
1092[1]	♂	May 26, 1909	44.8	13.1	17.5	5.5	4.5	12.0	11.4	17.6	17.5	13.3	26
255[3]	♂	June 22, 1908	44.6	13.8	18.8	5.8	4.0	12.1	9.6	20.2	21.7	11.0	28
254[3]	♂	June 22, 1908	44.8	14.0	18.8	6.4	4.2	12.5	10.2	19.0	18.8	11.0	28
253[3]	♂	June 22, 1908	45.8	13.7	19.0	6.0	4.5	12.8	11.5	18.8	18.0	10.8	29

[1] Vallecito, San Diego Co.
[2] Furnace Creek Ranch, Death Valley, Inyo Co.
[3] Carriso Creek Station, 3000 ft., Santa Rosa Mts.

Description of larva (based on material listed by Camp [1916*a*, p. 512] as probably pertaining to this species).—Greatest length of head-and-body 10.6 mm.; of tail 15.4 mm.; length of head-and-body contained 1.4 times in length of tail; width of body in head-and-body length about 1.9; nares about equidistant from orbit and tip of snout; internarial width about 1.3 in interorbital width; interorbital distance 4 to 7 in head-and-body length; eyes about 30 per cent of head-and-body length from tip of snout; spiraculum sinistral and lateral, aperture directed backward and slightly upward, center of aperture posterior to midpoint of head-and-body; anus median; tail moderate, height of muscular portion at base about 5 in length of tail.

Labial teeth in $\frac{2}{3}$ rows; first row complete, second divided, lowermost row shorter than two preceding; labial papillae only at sides of mouth region (fig. JJ).

Remarks on structure and coloration.—The following secondary sexual characters have been noted in the preserved specimens studied:

1. Males have the vocal sac at the base of the throat somewhat as in *Bufo cognatus*.

2. Males average darker in color than females although the extremes of the two sexes overlap.

3. The parotoid glands of males are, on the average, slightly higher than those of females.

4. Females average decidedly larger in all dimensions than males, as indicated in the accompanying table.

Dickerson (1906, p. 111) states that specimens from Lower California may be as large as 3 inches in total length and also may show a pattern of spots and stripes.

History.—This toad was originally described by Baird and Girard in 1852 from specimens collected by the United States and Mexican Boundary Survey, probably in Texas. Yarrow in 1882 (p. 441) described specimens from Lower California as *Bufo beldingi*.

Range.—*Bufo punctatus* occupies the deserts of southwestern United States and northern Mexico. It has been found east to central Texas as at Dallas, Waco (Strecker, 1915, p. 51), San Antonio (Cope, 1880, p. 29), San Diego (Cope, 1888, p. 395), and Fort Ringgold (Yarrow, 1883, p. 162). In old Mexico it has been found south to Guanajuato (Cope, *loc. cit.*), and in Lower California at numerous localities from the San Pedro Martir Mountains (Schmidt, 1922, p. 633) south to La Paz near the Cape (Yarrow, 1882, p. 441; 1883, pp. 162, 163). In New Mexico it has been recorded from Dry Cañon, near Alamogordo, Otero County, altitude 4600 to 5000 feet (Stone and Rehn, 1903, p. 34). In Colorado, Ellis and Henderson (1915, pp. 255–256) record *Bufo punctatus* from Basin Creek near the northern line of San Miguel County about 6 or 8 miles from Naturita, at an altitude of about 6500 feet. It is said to occur in Utah (Van Denburgh and Slevin, 1915, p. 100). In Arizona it has been listed from the Grand Cañon, between the Kaibab and Coconino plateaus (Stejneger, 1890, p. 117), and at several localities in the southern part of the state; Cave Creek, Maricopa County, in the foothills of the Catalina Mountains near Tucson, Pima County, and in Ramsey Cañon in the Huachucha Mountains (Van Denburgh and Slevin, 1913, p. 395).

Bufo punctatus was ascribed to California in 1859 by Heermann (1859, p. 24) on the basis of material collected by Möllhausen. Stejneger (1890, p. 117), however, indicates that this material probably pertained to the upper Colorado River in Arizona. The first definite record for *punctatus* in California is that by Stejneger (1893, p. 219) in the report of the Death Valley Expedition of 1891. The species has since been found to inhabit certain cañons on the east slope of the mountains in San Diego County at Vallecito, and on the north slope of the Santa Rosa Mountains in Riverside County (Grinnell and Camp, 1917, p. 144). Camp (1916*a*, p. 512) found this species in a cañon in the Turtle Mountains near Blythe Junction, San Bernardino County, and Stejneger (1893, p. 219) has recorded it from Furnace Creek in Death Valley and Cottonwood Cañon in the Panamint Mountains in Inyo County. The Museum of Vertebrate Zoology has a young specimen (no. 1841) from the Colorado River 20 miles above Picacho, on the California side.

The altitudinal range of the species is nearly 7000 feet. In Colorado it was found at an altitude of about 6500 feet, while in Death Valley it lives 200 feet or more below sea level.

Van Denburgh (1924, p. 195) lists this species as from Dog Spring and Dog Mountains, Hidalgo County, New Mexico, but I find no county of this name in that state. There is an Hidalgo County on the border close to Fort Ringgold in Texas.

Life-history.—*Bufo punctatus* is strictly a desert species, inhabiting practically the entire extent of the desert area in the southwestern United States and northern Mexico. Its occurrence is interrupted, the species being restricted to cañons where water is present in the limited amount necessary for its existence. The advent of irrigating systems developed since the country has been settled by Caucasians has probably been responsible for slight local increases in numbers, but no general increase in range can be attributed to this source.

The immediate habitat of the species is indicated by the following. Four specimens (nos. 253–256, Mus. Vert. Zool.) collected at Carrizo Creek, Riverside County, California, in the northern part of the Santa Rosa Mountains, about 12 miles southwest of Indio were found in a dry wash where an intermittent stream appeared above the surface of the ground for a short distance. Zonally the region is intermediate between arid Upper and Lower Sonoran, with a leaning toward the latter. Desert willow, a species of true willow, and arrowweed were conspicuous plants found there. The toads remained in

niches in the rocks during the daytime and came forth only at night, when they might venture as much as fifty feet from the water (Grinnell, MS). In Death Valley (Grinnell, MS) the species inhabits the irrigation ditches about Furnace Creek Ranch. Probably under original conditions there, it lived in the springs and overflow water from the springs. In a cañon of the Turtle Mountains, Camp (1916*a*, p. 512) found recently metamorphosed young toads huddled together in the crevices of planks about a pool and in wet sand nearby. Stone and Rehn in New Mexico (1903, p. 34) found two toads in a spring. Strecker (1915, p. 51) in Texas found many individuals under large flat stones in the bed of a small rock-bound creek.

Engelhardt (1917, p. 6) found *Bufo punctatus* at the Grand Cañon, Arizona, on June 9, 1916, in numbers. He says:

> *Bufo punctatus*, without doubt, is the most abundant of Batrachians in the Canyon, yet so secretive and strictly nocturnal is this toad, that none are likely to be encountered, except after dark. During the one night spent in the Canyon its call, mingling with that of *Hyla arenicolor*, was the dominant sound of animal life. Search for the toads with an acetylene lamp revealed such numbers that no attempt was made to count them. There were hundreds—many on the trail and many more in the shallow pools in the Indian Garden. None were seen mating, but their small black tadpoles, not exceeding half an inch in length, were swarming along the margin of the stream. Breeding evidently had taken place during May.

Of the notes of the adults he says: ". . . The call, though loud, is not harsh and consists of a series of deep, whistling notes, repeated at short intervals."

Strecker (1922, pp. 10–11) says that *Bufo punctatus*

> . . . is closely related to *Bufo debilis* but its habits are different from those of that species. *Debilis* prefers open country, usually mesquite-covered flats, and breeds in ditches and wayside pools. *Punctatus* is partial to rocky localities, especially high bluffs enclosing small streams. Here [central Texas] it breeds in rockbound pools. I have found specimens under rocks on the tops of cave-lined bluffs during the excessive heat of midsummer.

Van Denburgh and Slevin (1921, p. 54) state that at San Antonio in the Sierra Laguna Mountains of Lower California forty-six specimens of *Bufo punctatus* were taken around the public square of the village during the early evening (of one day?).

The voice of *Bufo punctatus* is described as "a long continued clear trill, resembling that of a hearth cricket but with more volume" (Grinnell, MS); Van Denburgh and Slevin (*loc. cit.*) say that at San Antonio, Lower California, the toads were heard calling late into the evening. A specimen captured there was observed to make a shrill

whistling noise of four or five seconds duration with about the same interval, the throat swelling considerably while doing so. Dickerson (1906, p. 112) says that the "dusky throat can extend into a large rounded vocal pouch."

The breeding season seems to be rather late, considering the nature of the territory occupied. In Death Valley the toads were in chorus and spawning at the end of the first week of April in 1917 (Grinnell, MS). In the Turtle Mountains Camp (1916*a*, p. 512) found larvae and some metamorphosed young toads on May 28, 1914, which he referred to this species. The metamorphosing young measured 9.4 to 10.5 millimeters in head-and-body length, and in life they were dotted on the back with many small red tubercles surrounded with indistinct black circles, a color pattern distinctive of the adults of *punctatus*.

The life-history in relation to the environment.—*Bufo punctatus* ranges over practically the entire desert area in the southwestern United States and northern Mexico. However, the proportion of the region actually occupied by this species is extremely small; its range is decidedly 'discontinuous.' The scarcity of records for *Bufo punctatus*, as compared, for example, with those for *Scaphiopus hammondii*, is striking. *Punctatus* was seldom found by early naturalists and even at the present time its stations of record are few and far between. The northern boundary of its range is still imperfectly known. Only in Death Valley and the Grand Cañon has this species been met with in any numbers. Ecologically, *punctatus* is restricted to desert cañons containing seepage or springs. Its present wide general distribution was probably accomplished at some time in the past, when less arid conditions prevailed on the southwestern deserts. The distribution of *Bufo punctatus* compares closely with that of *Hyla arenicolor* and the factors controlling the ranges of the two are probably somewhat similar. *Arenicolor* requires actual running water, whereas *punctatus* seems content with mere seepage, a later stage in the history of a regressive stream.

If, as is contended by some writers on southwestern climate (e.g., Huntington, 1914), the 'American deserts' are experiencing a progressive desiccation, then *Bufo punctatus* in particular among the desert amphibians is probably losing in numbers and territory as a species, for it apparently occupies an extreme position with regard to limitation in moisture requirements. If the evolution of the habitat precedes the evolution of the species, then removal of the habitat means disappearance of the species no matter how prolific or how

successful the individuals comprising it may be in meeting the other problems of existence. Practically all of the other Salientians which occur in the American southwest are restricted to the vicinity of the larger streams and they can continue there as long as these mountain-fed streams persist. *Bufo punctatus*, however, seems to be existing on a narrower margin of safety.

Bufo woodhousii Girard. Rocky Mountain Toad

(Pl. 11, fig. 31*b*, text fig. I)

Bufo dorsalis Hallowell (1852, pp. 181–182), not of Spix. Original description, type from "New Mexico" [= San Francisco Mountain, Arizona: see Stejneger, 1890, pp. 116–117].

Bufo woodhousii Girard (1854, p. 86). Name to replace *dorsalis*, preoccupied.

Bufo woodhousii, Cooper (1868, p. 486). Colorado (River) Valley.

Bufo lentiginosus woodhousii, Cope (1889, pp. 281–284, text fig. 69). General account.

Bufo lentiginosus woodhousii, Camp (1915, p. 332; 1916*a*, p. 509). Colorado River Valley; critical.

Bufo woodhousii, Grinnell and Camp (1917, p. 142, fig. 4). Range in California.

Bufo woodhousii, Stejneger and Barbour (1917, p. 29; 1923, p. 27). General range.

Diagnosis.—Size moderate to large, head-and-body length up to 81.8 millimeters (3¼ inches) [size still larger in specimens from eastern part of range]; cranial crests conspicuous, the longitudinal segments nearly parallel; parotoid glands twice as long as wide, divergent posteriorly and descending onto shoulders; warts on back conical, sharp-pointed, up to 3 mm. in diameter, distinctly encircled with black; two palmar tubercles; hind foot about three-fourths length of head-and-body.

Comparisons.—Distinguished from all other California Salientia except *Bufo cognatus* by well developed angular cranial crests in combination with long slender parotoid glands; from *Bufo cognatus* (both subspecies) by absence of conspicuous nasal boss, less divergent course of cranial crests, longer more slender parotoid glands, larger more conical dorsal warts, by absence of large blotches of dark color on dorsal surface, by proportionately longer hind foot, and by location of vocal sac of male on chin region adjacent to lower jaw (compare pl. 11, figs. 31*a*, 31*b*).

Description.—General form stout; muzzle oval in outline from above, bluntly rounded in profile; head thick through, greatest depth slightly more than one-half its length; external nares nearly terminal, apertures directed dorsolaterally; canthus rostralis usually distinct; orbit slightly less than one-half length of head; interorbital space varying from slightly less to slightly more than length of orbit, con-

cave in some individuals, convex in others; cranial crests well developed, longitudinal segments beginning just posterior to external nares, extending posteriorly in parallel course or slightly divergent; preorbital crest slight or wanting; transverse postorbital crest usually well developed, but short; tympanic membrane oval, decidedly higher than wide, vertical diameter about two-thirds length of orbit; parotoid gland close behind orbit, slender, about twice as long as wide, length nearly twice that of orbit, posterior ends of the two glands divergent; chin acuminate oval or roundly oval in outline; angle of jaw under tympanic membrane; vocal sac of male occupying entire chin region from margin of jaw posteriorly; about half of upper arm buried in skin; forearm about equal to hand; one large palmar tubercle, usually a smaller one at base of first digit, inner digit stoutest; digits in order of decreasing length, 3, 1, 4, 2; body slightly longer than broad; femur largely buried in skin of body; tibia equaling or slightly shorter than femur; tarsus about two-fifths length of foot; hind foot long, about three-fourths length of head-and-body; metatarsal tubercles two, outer small and rounded, inner large with distinct free cutting edge; toes small, in order of decreasing length, 4, 3, 5, 2, 1; web much restricted, edge slightly serrated.

Tongue moderate, less than half width of mouth at angles of jaws, cuneiform, attached by anterior two-thirds to floor of mouth; internal nares rounded, placed some distance back from margin of upper jaw.

Surfaces generally rough; tip of snout and immediate margin of upper jaw smooth; eyelids, dorsal and lateral surfaces of body, and exposed surfaces of limbs with many distinct conical, sharp-pointed warts up to 3 mm. in diameter, bases of adjacent warts sometimes confluent; warts larger and sharper on females than on males; plantar surface of hand and foot with numerous closely spaced smaller warts; ventral surface with fine even pattern of closely placed low conical or subconical warts, smallest and least rough on chin, largest and roughest at posterior end of body.

General body coloration above dull yellowish brown; narrow vertebral stripe whitish; larger warts or groups of warts on back narrowly surrounded with black; warts red-tipped; limbs obscurely barred with black; undersurface of body plain dull yellow, sometimes with small irregular markings of black on breast; tips of fingers and toes dark brown or blackish; larger tubercles on plantar surface of hand and foot dark yellowish brown; metatarsal tubercles yellowish brown at base, black at tips; iris in life metallic yellow (color description partly adapted from Dickerson, 1906, p. 91).

Stejneger (1890, p. 116) describes two "medium-sized" specimens from Tanner's Gulch, 3 miles north of Tuba City, Painted Desert [= east-central Coconino County], Arizona, as follows: "Above pale olive-green with a somewhat lighter stripe down the middle of the back; tip of tubercles pale red surrounded by black rings; lower surface olive-white." Two other much smaller [yearling?] specimens taken at "Tanner's Crossing of the Little Colorado" in the same vicinity are described in detail as follows:

Entire upper surface pale flesh color, suffused with buff on hands and feet; parotoids darker, nearly "brick-red" except in the middle; all the tubercles of the same red color; each of the larger ones surrounded at the base by a circle of minute black specks; a narrow white stripe down the middle of the back; a few dusky annular marks on upper flanks and hind legs; under surface bluish-white; lower abdomen and inner side of hind limbs pale brownish-yellow; palms of the same color, but the inner surface of the fore limbs pinkish; iris brassy, densely clouded with dark mottlings, except a narrow inner ring which is bright metallic.

MEASUREMENTS OF ADULT SPECIMENS OF *Bufo woodhousii* FROM SOUTHWESTERN UNITED STATES

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
7693	♀	Chandler, Maricopa Co., Ariz.	Sept. 8, 1919	72 5	20 6	27.8	9.5	5.0	17.8	18.0	27 0	27.0	16.7	45
1844	♀	Potholes, Colorado River, Calif.	Apr. 27, 1910	79 6	22 2	31.2	10.5	3.8	19.3	22.6	35.8	32.8	20.7	53
1842	♀	Potholes, Colorado River, Calif.	Apr. 28, 1910	81.8	23 7	34.0	11.0	5.0	22.6	21 7	36.9	35.4	21 3	57
5552	♀	Albuquerque, N. M.	about Aug. 5, 1914	82.2	23.6	33.0	10.0	6 2	23.5	23.0	38 0	35.0	21.5	60
7691	♀	1 mi. e. Willcox, Cochise Co., Ariz.	Aug. 3, 1919	84.6	23 5	32 8	10 4	4.2	21 8	20.0	36 0	33.7	20.0	56
8919	♂	Bunkerville, Lincoln Co., Nev.	Mar. 28, 1923	56.0	17.0	23.3	7 7	4 7	16.0	15.5	24 0	23.0	14.0	41
8909	♂	Bunkerville, Lincoln Co., Nev.	Mar. 28, 1923	60.0	18 0	25 0	9.0	5.0	17.0	16.3	28 5	24.2	15.6	42
8921	♂	Bunkerville, Lincoln Co., Nev.	Mar. 28, 1923	62.0	19.3	26.0	10.0	5.0	17.7	18.2	25.5	26.0	16.7	45
8531	♂	Albuquerque, N. M.	June 1, 1902	68.5	20.5	26.8	9.4	4.2	18.5	18.7	29.0	29.0	17.2	47
7692	♂	Willcox, Cochise Co., Ariz.	Aug. 3, 1919	76.8	22.5	29.0	10.2	5 0	21.2	18 7	33.6	31.2	19.0	52

History.—This toad was originally described as *Bufo dorsalis* by Hallowell in 1852 on the basis of a specimen obtained by Dr. S. W. Woodhouse on "San Francisco Mountain, New Mexico." The name *dorsalis* being preoccupied by an earlier name given by Spix, Girard in 1854 rechristened the species *woodhousii*. Stejneger (1890, pp. 116–117; compare Cope, 1891, pp. 1204–1205) has shown that these two names apply to one and the same specimen. The limits of New Mexico, at the time of Woodhouse's exploration, extended to the Colorado River and it was not until 1863 that the western part of the area, including San Francisco Mountain, was separated to form the Territory (now State) of Arizona (see Van Denburgh, 1924, pp. 189–190). *Woodhousii* has until recently usually been considered a western subspecies of *Bufo lentiginosus* [= *americanus*], but structurally

the two present certain points of difference. The fact that the two occur on common ground as in Colorado is an additional argument for specific distinctness. Cope's (1866*b*) *Bufo frontosus* belongs here.

Range.—*Bufo woodhousii,* while called the Rocky Mountain Toad, occupies a somewhat greater extent of territory than is indicated by its vernacular name. It is the characteristic species throughout the southern part of the Rockies. The northward extent of its distribution is as yet not well known. Fort Custer, Montana (Cope, 1889, p. 284), seems to be the most northerly record to date. Cary (1917, pp. 27, 33) lists this species as occurring in the Upper Sonoran and Transition zones of Wyoming, but without specific localities; Cope (*loc. cit.*) gives Fort Laramie as a locality of record. In Colorado, *woodhousii* is present in many places from Greeley and Grand Junction south to Durango and Lamar (Ellis and Henderson, 1913, pp. 54–55). It has been recorded from Nebraska at "swamps on Loup Fork" and from "Kansas" (Cope, *loc. cit.*). The material from these localities would seem to need reëxamination. In Texas, Strecker (1915, p. 53) restricts *woodhousii* to the extreme western end of the state in Brewster and Jeff Davis counties and at El Paso; this author, who considers *woodhousii* as a subspecies of *lentiginosus*, discusses Dickerson's (1906, pls. 25, 26) record for Fort Worth under *americanus*. *Woodhousii* seems to be widespread in New Mexico from the Rio Grande River westward to Grant County and to Fort Wingate (Van Denburgh, 1924, p. 197; *et al.*). In Arizona it has been found south to Willcox, Cochise County (Mus. Vert. Zool.), Camp Crittenden (Yarrow, 1875, p. 521), and Yuma (Van Denburgh and Slevin, 1913, p. 394). It ranges into southern Nevada in Lincoln County at Caliente (Stone, 1911, p. 223), Bunkerville (Mus. Vert. Zool.), and Pahranagat and Vegas valleys (Stejneger, 1893, p. 221). In Utah it has been found at Fort Douglas near Salt Lake City and in other localities to the eastward (Van Denburgh and Slevin, 1915, pp. 101–102), and at Bellevue, Washington County (Engelhardt, 1918, p. 78).

In California, *Bufo woodhousii* is restricted to the extreme southeastern corner of the State along the Colorado River where it has been found at Potholes and 5 miles northeast of Yuma on the California side (Grinnell and Camp, 1917, p. 142).

Dickerson (1906, p. 93) states that the vocal sac of this species can be extended into a rounded throat pouch. The call [of the male] is a vibrated note of high pitch and sweet quality. It is said to resemble that of *americanus* and *lentiginosus,* which fact this writer

takes as proof of common ancestry. The distinction between *woodhousii* and *cognatus* has been indicated in the present paper in the paragraphs on "Comparisons."

Ruthven (1907, p. 508) says that at Alamogordo, Otero County, New Mexico, all the specimens of *woodhousii* which he obtained

. . . were taken in the evening along irrigating ditches in the Mesquite association on the plains. As in the case of *B. punctatus*, the natural habitat of var. *woodhousii* is probably the cañons in the mountains, where moisture is more abundant, and it can be considered to have extended its range out onto the plain with the advent of irrigating ditches. . . . During the intense heat of the day these toads were not seen, but about dusk they came out in numbers along the shallow ditches, especially near street lamps.

Beetles there make up the bulk of the food.

At Bellevue, Washington County, Utah, altitude 4000 feet, this species was found breeding "during May [1917] in irrigation ditches and springs" (Engelhardt, 1918, p. 78).

Pack (1922, pp. 46–47) has described the response of a toad population comprised of *Bufo woodhousii* to an outbreak of sugar-beet webworm in Cache, Utah, during August, 1921.

Most of the toads were of this year's brood, ranging in length from one and a fourth to one and a half inches. I would estimate that in one field of about one square acre there were no fewer than one hundred toads.

An examination of the stomach contents of a number of toads disclosed the fact that they were feeding exclusively upon the webworms and that every one was gorged to the limit. These small toads contained from 24 to 40 worms each, the limiting factor in quantity being the size of the stomach. A number of representative toads were weighed, and the stomach contents of each were then removed and weighed. It was found that the contained food represented 16 per cent of the total weight of the toad. . . .

From this case it would appear that the toad exhibits the same valuable adaptibility in the presence of an insect outbreak as has been observed in birds. Not only is there a concentration in numbers of toads in the infested area, but the dominating insect, especially if present in great numbers, is eaten almost to the exclusion of the insects and other invertebrates normally constituting its food.

Hyla arenicolor Cope. Cañon Tree-toad

(Pl. 2, fig. 4; pl. 13, figs. 37–39; text figs. Z, LL)

Hyla affinis Baird (1854, p. 61). Original description, type from northern Sonora, Mexico.

Hyla arenicolor Cope (1866*a*, p. 84). Name to replace *affinis*, preoccupied.

Hyla arenicolor, Yarrow (1883, pp. 24, 175). Range.

Hyla arenicolor, Cope (1889, pp. 369–370, text fig. 93). General account.

Hyla arenicolor, Dickerson (1906, pp. 122–123, pl. 48). General account.

Hyla arenicolor, Richardson (1912, pp. 605–611, 1 text fig.). Range in California and elsewhere.

Hyla arenicolor, Stejneger and Barbour (1917, p. 32; 1923, p. 29). General range.
Hyla arenicolor, Grinnell and Camp (1917, p. 145). Range in California.
Hyla arenicolor, Stephens (1921, p. 6). In San Diego County.

Diagnosis.—Size small, head-and-body length 50 millimeters (2 inches) or less; fingers and toes with expanded adhesive discs; no webs between fingers; dorsal skin rough-surfaced, with many small papillae; side of head concolor with rest of head and body; coloration light or dark gray.

Comparisons.—Distinguished from other Salientia of California by expanded discs on fingers and toes and by small size of adults; from *Hyla regilla* by average larger size (especially of females), by larger discs on digits, by rougher skin on dorsal surface of body and by lack of dark stripe on side of head through eye.

Description.—Form stout for a *Hyla;* head flat, muzzle rounded in profile, pointedly oval in outline from above; canthus rostralis slightly longer than diameter of orbit; external naris on canthus rostralis, close to tip of snout; orbit moderate in size; interorbital space flat, slightly wider than width of one eyelid; tympanic membrane inconspicuous, smooth-surfaced, oval in outline, wider than high, width not more than half length of orbit; a thickened fold of skin extending from behind orbit around dorsal and posterior margins of tympanic membrane; pectoral fold of skin on breast in line with axillae; upper arm more slender than forearm; one large alongate tubercle on inner margin of palm; sesamoid tubercles numerous; digits stout, without webs at base, in order of decreasing length, 3, 4, 2, 1, expanded tips about twice diameter of digits; hind legs moderate; femur shorter than tibia; entire foot one-third longer than tibia; tarsus about two-fifths length of entire foot; one elongate tubercle on inner margin of metatarsus; toes stout, in order of decreasing length, 4, 5, 3, 2, 1; webs moderate, two phalanges of fourth toe free; discs on toes wider than long.

Tongue nearly filling lower jaw, attached for anterior two-thirds of its length; internal nares but slightly posterior to margin of upper jaw and well separated; vomerine teeth in two small clusters between internal nares.

Skin on dorsal and lateral surfaces of head and body and on exposed surfaces of limbs and digits with many low papillae, larger, more numerous and more conspicuous on females than on males; ventral surface of body areolate.

Ground color of dorsal and lateral surfaces (in life) varying from very pale gray to dark gray, usually of medium tone ('granite gray'), marked with irregular small blotches of darker gray; middle of each eyelid crossed by a dark bar, the two sometimes meeting on interorbital space; exposed surfaces of limbs with crossbars of dark gray, three each on femur and tibia, two on forearm; ventral surface of body, pale yellow; concealed surfaces of hind leg, orange; loose skin of vocal sac on throat of male, blackish.

Description of larva.—(No specimen is available in the proper stage of development for adequate description of the larva [the third

stage of Dugès, with hind limbs developing]. The following description and measurements apply to an individual collected in Palm Cañon, Riverside County, March 26, 1923, which was only 14.7 millimeters in total length.) Length of head-and-body 6.45 mm.; of tail 7.80 mm.; length of head-and-body contained 1.2 times in length of tail; tip of snout to orbit 4.8 in length of head-and-body; greatest width of body 1.6 in its own length; greatest height of body 1.75 in its own length; interorbital space 4.1 in length of head-and-body; spiraculum sinistral, aperture directed backward; center of aperture slightly behind midpoint of body; anus dextral. Skin brownish black with numerous minute xanthophores (0.05 mm.) scattered over surface; tail banded with yellow and black.

MEASUREMENTS OF ADULT SPECIMENS OF *Hyla arenicolor* FROM FOOTHILL CAÑONS IN VICINITY OF SIERRA MADRE, LOS ANGELES COUNTY, CALIFORNIA

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4430[1]	♀	May 1, 1909	40.5	12.5	15.2	4 7	3.2	9.5	11.8	19.3	23.0	13.0	31
4421	♀	Apr. 11, 1908	41.0	12.5	15.3	5.2	3.0	9.0	12.3	20.4	22.0	12.8	31
4426	♀	Apr. 25, 1908	41.0	12.5	14.5	5.5	3.3	9.0	14.0	20.3	21.5	12.5	28
4427	♀	Apr. 10, 1909	41.5	13.0	15.0	5.5	3.0	9.5	13.5	18.0	21.0	12.0	28
4415	♀	Apr. 5, 1908	43.2	13.1	16.3	5.0	3.0	9.6	12.0	21.0	22.3	13,3	29
4424	♂	Apr. 20, 1908	30.0	10.0	11.0	4.6	3.0	6.7	9.0	16.3	17.3	10.0	24
4417	♂	Apr. 5, 1908	30.8	10.3	12.3	4.1	2.4	7.6	9.0	15.0	16.4	9.5	22
4414	♂	Apr. 5, 1908	31.4	10.4	11.7	3.7	2.3	7.6	9.0	15.0	17.8	10.0	23
4428[1]	♂	May 1, 1909	32.0	10.3	11.3	4.0	2.8	6.8	10.0	15.5	16.8	9.3	23
4418	♂	Apr. 5, 1908	33.8	11.3	12.5	4.4	3.2	8.0	10.0	15.0	18.0	10.0	24

[1] W. fork San Gabriel River, 3000 ft.

Remarks on coloration.—This *Hyla* possesses some power of color change, though the range is much shorter than in the case of *Hyla regilla,* as its colors are always some tone of gray. Individuals of *arenicolor* are at times almost white in ground color; again, the same animal may be very dark gray. The usual color is, however, a gray of medium tone, closely resembling that of the granite boulders on which the animals rest. Dickerson (1906, p. 123) says of examples taken at Tucson, Arizona, "The colour is rapidly changeable from gray or brown so dark that it is nearly black, through distinctly spotted phases, to a pinkish or grayish unspotted white."

The present writer has not seen the brownish tones in living California specimens, though his experience with the species in life has been limited. Alcoholic specimens are usually gray; occasional

individuals are seen in preservative which are very dark brown. The orange color on the hind legs and the black on the throat of the males are colors which are apt to disappear after several years of preservation.

History.—This distinctive species was first described by Baird in 1854 on the basis of a specimen received from somewhere in the northern part of the Province of Sonora, Mexico. Baird's name *affinis* (probably an allusion to the similarity between this species and the eastern *versicolor*) proved to be preoccupied by an older name used by Spix, in consequence of which Cope in 1866 renamed the present form with the appropriate designation, *arenicolor.*

Range.—This is a wide-ranging species, having been found as far east as Del Rio, Texas (Stone, 1903, p. 539), south in Mexico to Guanajuata, and possibly to the neighborhood of Mexico City (Cope, 1885, p. 387; 1887*b*, p. 14), and north to Santa Fe, New Mexico (Yarrow, 1875, p. 524), and to the Grand Cañon of the Colorado near the Coconino Plateau, Arizona (Stejneger, 1890, pp. 117–118). On the west it ranges through the mountains of southern California from Mountain Spring (Richardson, 1912, p. 606) and Mission Valley near San Diego (Storer, MS), to Little Rock Creek, Los Angeles County, and to Nordhoff, Ventura County (Grinnell and Camp, 1917, p. 145). Yarrow's (1875, p. 524) ascription of the species to Utah has been confirmed by Englehardt (1918, p. 79) who found it "common about springs, irrigation ditches, and rapidly flowing streams" in the vicinity of Bellevue, Washington County, altitude 4000 feet, on streams tributary to the Colorado River. Van Denburgh and Slevin (1921*c*, p. 54) record it from Ensenada, Lower California.

Life-history.—Differing markedly from its one Pacific Coast congener, *Hyla arenicolor* is highly restricted ecologically. It is a cañon species living chiefly on the boulders which line the courses of the streams which come down out of the mountains in the southwestern desert area. During the daytime (at least of the spring months) these hylas rest in niches on the surfaces of the boulders. I do not recall having seen one more than 12 inches away from the edge of a running stream. Their resting places vary from one inch or two up to perhaps 24 inches above the water. When on the rocks the hylas crouch down with their legs and feet folded in beside or beneath the body. Out of the water the skin becomes slightly dulled and the irregular surface with its numerous small warts tends to break up mass reflections such as would come from a smooth-skinned amphibian under similar cir-

cumstances. In outline and in coloration these hylas simulate their environment, so that, to the human eye, they may pass as small protuberances on the rocks. (Compare pl. 2, fig. 4, and pl. 13, figs. 37, 38.) Indeed, if a person is seeking to collect these hylas it is often desirable to stand and give close scrutiny to the rocks close at hand, whereupon one or more hylas will often be discerned where a hasty glance might have failed to detect them. As part of this scheme which results in the animals escaping observation, they remain absolutely quiet, even on the close approach of a person, so that it is often possible to walk slowly but directly up to where one of the animals is located and with a quick movement capture it in place.

On March 25 and 26, 1923, I visited the lower reaches of Tahquitz Creek, near Palm Springs, Riverside County, for the purpose of studying the habits of *arenicolor*. The creek is inhabited by this hyla down almost to where the waters disappear into the sands of the Coahuilla Desert. During the day the hylas did not come particularly to notice, except when hunted for, but with the approach of evening the voices of the males were much in evidence.

Many of the creeks which come down from the mountains of southern California have their sources during the winter and spring months in banks of snow. When the sun leaves the mountain in the afternoon the melting of the snow lessens or stops and the creeks carry slightly lesser quantities of water. Their courses being short, the water in the desert end of the streams soon drops an inch or so. The males of *Hyla arenicolor* then take position for the nightly chorus. Usually they sit solitarily on the narrow strip of wet sand left exposed along the bank by the lowering of the water; occasionally one takes shelter in a crevice between two rocks. In practically all cases there is a rock above the animal which acts as a shelter against the approach of enemies from the shore side and also probably serves to some extent as a sound reflector. The male hylas sit with their backs to the shore, facing the stream, toward the center of which they direct their vocal effort. (The females of this species are not known to leave the creek at any time.) Each male sits with hind legs in the usual position with 'knee-joints' out and tarsi touching, while the front feet are beneath the body but with the legs spread apart so as to leave space beneath the front of the body. This brings the chin up so that the vocal pouch does not touch surrounding objects when it is expanded. These animals do not croak so persistently as *Hyla regilla*. One individual will give ten to fifteen notes, then have a quiet spell of

varying length, after which it will croak again. Often a small basin or pool on the course of the stream will have several males about it. These all face inward toward the center and tend to join together for a series of notes, then all are quiet for a time. But this is not an invariable rule. The notes carry well, so that to an observer stationed at any one point there are always hylas in voice. In fact along Tahquitz Creek on the night of March 25 there was a regular 'background' of hyla voices. In the quiet periods the animals keep their pouches partly distended. The note is a single utterance, resembling the *quack* of a duck (though not so blatant as that of a Mallard). Camp (MS) writes it *cherk*. According to Cope (1887, p. 14), Dugés states that in Mexico the note reminded him of the bleat of a goat.

Engelhardt (1917, p. 6) says that the note of *Hyla arenicolor* "is lower in pitch, but is otherwise very much like the bleating notes of *Hyla versicolor.*" The note differs markedly from that of our common western tree-toad (*Hyla regilla*) in being lower in pitch, somewhat weaker in volume, and without any tendency toward a two-syllable sound such as is heard often from *regilla*. On two occasions, in San Diego County, the two species were heard side by side and there was not the slightest difficulty in distinguishing them. Two separate individuals of *arenicolor* which were timed by the watch were croaking at one-second intervals. With all the males noted on Tahquitz Creek (fully 25 were located) only one female was seen. The chorus began about 4 P.M., soon after the sun had disappeared behind the San Jacinto Range, was strongest just after dark, from about 7:30 to 8:30 P.M., and continued on into the night at least until 2 A.M. On other occasions males of *Hyla arenicolor* were heard croaking up to about 6 A.M., but only a few notes were given as late as that hour in the morning. The duration of the 'song' season is unknown; on the morning of June 21, 1919, Cañon Tree-toads were heard croaking in cañons near the Mount Wilson trail. Dickerson (1906, p. 123) says "both male and female give a sharp high-pitched cry when taken in hand." The present writer has not heard this note, though he handled upwards of 25 of the animals in the field during 1923.

The writer searched a number of creeks in southern California during March and April, 1923, in an effort to find the eggs of this species, but without avail. Miss Sarah R. Atsatt lent her efforts in this search with good result. On March 26, 1923, Miss Atsatt found a number of tadpoles in the upper reaches of Palm Cañon Creek, Riverside County. These proved to be *Hyla* larvae, not of *regilla,* and

hence, by reason of the fact that only two hylids occur in the region, they were believed to be those of *Hyla arenicolor*. At the same time one solitary egg in a spherical capsule was collected. Nothing was then known of the nature of the eggs of *arenicolor*, and the solitary egg was considered to have been deposited separately by accident, as sometimes is done by *H. regilla*. But subsequent findings showed that this egg was deposited in a thoroughly characteristic manner. Miss Atsatt continued to search the creeks for eggs of *Hyla arenicolor* and on April 15, 1923, she found eggs of this species spawned under natural conditions in Snow Creek, on the south side of San Gorgonio Pass, in Riverside County. Some of these, together with other eggs spawned in captivity, and with some of the adult animals, were forwarded to the writer at Berkeley for study. The field notes incorporated herein, were, except where otherwise indicated, furnished by Miss Atsatt.

An examination of Snow Creek on April 14 to 16, 1923, indicated that the breeding season of *Hyla arenicolor* was at its height. Adult specimens of this species together with some small individuals of *Rana boylii muscosa* were found in a series of pools adjacent to the main creek. Some of the hylas were collected and placed together in a can on the night of April 14–15, and the next morning a mass of eggs was found with the hylas. This prompted search of the pools for naturally spawned eggs which were soon discovered. The first eggs to be found were attached to the upper surface of some sycamore leaves which had fallen the previous autumn and lay unrotted, in the bottom of a pool (pl. 13, fig. 39). Then other eggs were found floating near the surface of the water, and still others on the bottom of the pool. A few were found attached to the undersurfaces of leaves in the pond.

The eggs are extruded singly [like those of the Eastern Peeper, *Hyla pickeringi*], and the jelly coat is very sticky so that when an egg touches any object it at once becomes affixed. Either the spawning animal moves about a good deal while the eggs are being laid, or, if she remains in one position, the eggs are extruded singly and dispersed by the current of the stream. That some sort of scattering of the eggs is operative was indicated by the finding of about twenty fresh eggs distributed over an area about two feet square. When the eggs are laid in the confines of a small container, even though extruded singly they adhere together in a way which was not found to occur under natural conditions. The sticky condition of the jelly continues

for some time after the eggs are laid, as some eggs which were laid in a glass jar on the night of April 15–16, and which were separate when turned into a pan of water the next morning, immediately became affixed to the bottom of the pan.

Some of the eggs found in the stream on the morning of April 15 were in the four-cell stage and hence had been laid during the preceding night. Only two or three tadpoles of *Hyla arenicolor* were seen where the egg masses were collected. None of the adult hylas were found in the water of the stream during the day save when frightened there by the movements of the observer. They were all, as is their custom at other times of the year, on the sides of the granite rocks bordering or in the stream (Atsatt, *in letter*).

The jelly coat surrounding the egg of *Hyla arenicolor* is colorless when the egg is laid and would doubtless continue so if it did not gather a coating of fine sediment and débris from the water. So far as I can determine there is but one coat of jelly. Typically, this is perfectly spherical.

A number of the eggs laid in captivity on the night of April 15–16, 1923, by adults taken from Snow Creek, were preserved in 5 per cent formalin on the following morning. These now present the following measurements, in millimeters:

	Egg	Jelly coat
Minimum	1.83	4.14
Maximum	2.10	4.68
Average of 15	1.95	4.39

The vitelline space surrounding the egg measures about 0.1 millimeter more than the egg itself (fig. Z). Discoloration of the surface of the jelly coat made it impracticable to measure accurately the vitelline capsule in most of the eggs at hand.

Another smaller series of eggs, some of which were spawned while the animals were en route by express from Los Angeles to Berkeley, and which were infertile, gave the following measurements, in millimeters:

	Egg	Jelly coat
Minimum	1.88	3.87
Maximum	2.42	5.00
Average of 5	2.19	4.41

From some of the eggs which were collected on April 14 and 15 three larvae were hatched on or about April 20. These measured as follows: Total length 8.1 millimeters; length of head-and-body 3.2 to 3.6 mm.; greatest height of body 1.0 mm.; height of caudal fin at anus 1.3 mm.; tip of snout to orbit 0.4 mm.; interorbital width 0.6 mm. The general coloration was dull yellow, suffused with dusky on the back and along the sides of the caudal myomeres. On one larva, slightly older, the lateral surface of the tail was marked by aggregations of dark pigment with intervals of the prevailing yellow between. This is the forerunner of a conspicuous cross-banding of the tail which characterizes the larva of more advanced age.

Definite information on the life-history practically ceases with the data on the larvae reared from the eggs found in Snow Creek and the larvae from Palm Cañon.

Females taken at Sierra Madre on April 5, 1908, April 10, 1909, April 25, 1908, May 1, 1909, May 20, 1913, and May 30, 1918, contained eggs of large size. In one female secured on the last named date the eggs were already in process of resorption. These data suggest that the spawning observed in 1923 was probably at the middle of the breeding season. A female taken at Sierra Madre on April 11, 1908, and two secured in Lower Murray Cañon, Riverside County, on April 7, 1918, were 'spent.' One nearly metamorphosed young hyla, with a mere stub of a tail remaining, was taken at La Puerta, San Diego County, on June 5, 1909; its head-and-body length is 17 millimeters. This indicates that the larval life, as with *Rana boylii boylii*, is probably short. Three fully metamorphosed young individuals of the present species collected in the Arroyo Seco near Pasadena, Los Angeles County, on August 23, 1903, now measure 18.0, 19.4 and 20.3 millimeters in head-and-body length. Two specimens from a spring on Pine Mountain at 2750 feet altitude near Escondido, San Diego County, collected September 4, 1906, are respectively, 22 and 23.6 millimeters long. It would seem that but little growth is accomplished in the autumn after metamorphosis. Thus, an individual collected in Tujunga Cañon, Los Angeles County, "4/1/04" [probably April 1, 1904] is only 23.3 millimeters in head-and-body length. One taken near Sierra Madre on April 5, 1908, measures 20.2 millimeters, and another collected there on May 20, 1913, was 28 millimeters long in life, and now, in alcohol, measures 26.4 millimeters.

I am unable to find more than two size-groups in the metamorphosed individuals at hand, which suggests that *Hyla arenicolor* reaches its adult size and breeds when two years old. The breeding animals collected April 15, 1923, on Snow Creek are about the size of the smallest individuals listed in the table of measurements given above.

Wright (1920, pl. XVII, fig. 2) has figured some eggs which are labeled "The stalked eggs of the desert tree toad (?)." There was evidently doubt in his mind as to the exact identity of the eggs. I am loath to believe that the eggs figured could be those of *Hyla arenicolor*. The figure is not clear but the stalking is evident. None of the water-spawning salientians with which I am familiar produce pedunculated eggs.

Englehardt (1917, pp. 5–6) found *Hyla arenicolor* abundant in clear shallow pools on the course of a creek near the Bright Angel trail in the Grand Cañon of the Colorado, Arizona. On June 9 and 10, 1916, the tree-toads were numerous and some were still mating. No ova, but many tadpoles, were found in the water. "The tadpoles were about one inch long [thus probably about two-thirds grown]; uniformly dark gray above and iridescent light gray below; tail broad, heavily marbled, dark gray; eyes golden." The same author (Englehardt, 1918, p. 79) makes the statement that near Bellevue, Washington County, Utah, in [May or June?] 1917, "ova [presumed to be of this species] were observed in the form of small clusters deposited along the margin of pools. The tadpoles, at first black, later become mottled gray when they resort to deeper water."

The life-history in relation to the environment.—The range of *Hyla arenicolor* is a splendid example of local discontinuous distribution. Although its general range extends from Texas to the Pacific Ocean and from central Mexico to Utah, the actual area occupied by the species is only a very small portion of the territory indicated. Within the mountains of southern California it is an inhabitant of many cañons. From the eastern scarp of the San Jacinto Mountains and the mountains of eastern San Diego County there is a big gap to the eastward which, so far as present information indicates, is entirely uninhabited by the species. The next nearest station of record is Fort Whipple, Arizona. The condition indicated for California obtains throughout the entire range of the species. Its actual territory of occupation is quite 'spotty.' Thus far no differences worthy of nomenclatural recognition have been advanced to separate any of the

local colonies of this amphibian, although a large series of specimens from appropriate localities might be found to exhibit geographic variation. The fact that no differences have been pointed out by systematic herpetologists suggests that the species must be quite uniform over its vast range, or at least that it presents no variations which can be correlated with geography. This would argue that its present 'patchy' mode of distribution is an event of rather recent time, geologically speaking, or else that the species is very conservative as to change.

Geologists believe that the mountain ranges lying east of the Los Angeles plains are of very recent origin, that a relatively short time ago these ranges were much lower or lacking. When such conditions obtained there were probably streams, some of which were perennial, on a number of the mountain ranges in the deserts of southeastern California where no such creeks exist today. A species of creek-dwelling amphibian could pass across a series of such streams in adjacent mountain ranges in a comparatively short span of time by means of the connections set up when sudden heavy rains occur, whereas present conditions would seem to be entirely against such dispersal. The desert tongues of the streams which come down out of the southern California mountains each season change markedly in extent. In wet years they are long, in dry years short, and there is a progressive seasonal shortening in any one year through spring, summer, and autumn, until the advent of the next rainy period. The Cañon Tree-toads evidently move down and back with the fluctuations in the stream, as observers who have visited Tahquitz Creek in the later seasons of the year have found it dry in parts where hylas are present in numbers in the spring months. Pressure from competition for food, or the natural tendency of a species to spread out and occupy all regions which it can tolerate probably accounts for this spreading even within the compass of a single year. In the event of a cloudburst in a semidesert region the streams are swollen to many times their normal volume. Animals like *arenicolor* would be swept down and away from their native cañons onto the common grounds below. As the water receded they would tend to follow it backward, but not all would necessarily get back to their own streams (this despite the strong homing instinct which is argued by some persons for at least certain of the Salientia). They would follow the retreating creeks and new creeks would thus be populated. Given the numerous occurrences of this sort which would happen over a brief period

of time geologically speaking, and the spread of an amphibian, even one as restricted ecologically as is *Hyla arenicolor*, could be accounted for readily.

The habit of *arenicolor* of occupying the surfaces of rocks adjacent to and over the actual course of the stream probably permits the animals to 'keep in touch,' so to speak, with the stream. Were the animals to take shelter in crevices in rocks, as *Hyla regilla* sometimes does, a few days of aestivation in such a location during the season when the stream was in retreat might mean their separation from water to a distance too great to be covered before the toad perished from desiccation.

Presuming for the time being that the spread and reinvasion of the species operates in the manner indicated it would seem that the deposition of solitary eggs would be of further survival benefit to the species. Such eggs would in a sudden increase of water be less likely to be damaged than if they were in a large mass and subject to the buffeting of a sudden torrent. If it is a regular circumstance for the eggs to become attached to dead leaves in the water there would be more likelihood of their being carried on the surface of the current and hence less chance of their being damaged than if they were attached to small rocks in the stream bed.

The evidence at hand suggests a late date of spawning and an early season for transformation, in other words, a short period in the critical and to the individual rather dangerous tadpole stage. No exact counts of eggs laid by single females are at hand, but the number of ovarian eggs seen in several separate specimens would suggest a complement of several hundred eggs. This, in conjunction with the rather large population of breeding adults which is found along the foothill creeks in the spring (and which is not a 'concentrated' population from over a wide feeding area as in *Hyla regilla*, but the regular population of the creek), would suggest that the mortality is high at one or more stages in the life-history.

It seems reasonable to expect that the seasonal program of *Hyla arenicolor* in the mountain and foothill cañons of southern California is to a considerable degree controlled by water conditions. The same factors which seem to be operative in the case of *Rana boylii boylii* (see p. 259) would seem to be of importance here. Freezing of the water practically never occurs in the southern California streams, but the water supply may lessen so that the creeks retreat up into the mountains. The emergency which *Hyla arenicolor* has to meet then is that of drought instead of freezing. Temperature undoubtedly plays

a part, just how important a part it is impossible to say with our present incomplete knowledge. Before the relative importance of these two factors can be determined we need to know something of the temperature cycle and heat quotient of the streams, and we also need data on the complete seasonal schedule of *Hyla arenicolor* in some one locality. But that moisture conditions play a very important part seems an unavoidable conclusion.

Hyla regilla Baird and Girard. Pacific Tree-toad

(Pl. 3, fig. 5; pl. 6, fig. 12; pl. 14, figs. 40–42; pl. 16, fig. 49 [upper left figs.]; text figs. Y, GG)

Hyla regilla Baird and Girard (1852*b*, p. 174). Original description, type from Sacramento River, California.

Hyla scapularis Hallowell (1854, p. 96). Type locality, Tejon Pass, California.

Hyla nebulosa Hallowell (1854, pp. 96–97). Type locality, Tejon Pass, probably near Fort Tejon, Kern County, California.

Hyla scapularis var. *hypochondriaca* Hallowell (1854, p. 97). Type locality, Tejon Pass, California.

Hyla cadaverina Cope (1866*a*, p. 84). Name to replace *nebulosa* Hallowell, preoccupied.

Hyla regilla, Cooper (1868, p. 485). General range.

Hyla regilla, Yarrow and Henshaw (1878, p. 208). Locality records.

Hyla regilla, Boulenger (1882*a*, p. 374). General account.

Hyla regilla, Yarrow (1883, pp. 24, 171, 172). Locality records.

Hyla curta, Yarrow (1883, pp. 24, 171). Locality record.

Hyla regilla, Cope (1889, pp. 355–361, text fig. 89). General account.

Hyla regilla, Stejneger (1893, pp. 222–224). Locality records in eastern California and Nevada.

Hyla curta, Van Denburgh (1895*a*, pp. 557–558). Application of name.

Hyla regilla, Test (1898, pp. 477–492, pl. 39). Critical; coloration; measurements; range.

Hyla regilla, Van Denburgh (1905, pp. 3, 13, 23). On coastal islands.

Hyla regilla, Dickerson (1906, pp. 4, 41, 134–138, col. pls. 8, 9, pl. 53 [figs. 165–169]). General account.

Hyla regilla, Van Denburgh and Slevin (1914, pp. 132, 135, 137, 144). On coastal islands.

Hyla regilla, Grinnell and Camp (1917, pp. 144–145). Range in California.

Hyla regilla, Stejneger and Barbour (1917, p. 33; 1923, p. 31). General range.

Hyla regilla, Stephens (1921, p. 60). Range in San Diego County.

Hyla regilla, Grinnell and Storer (1924, pp. 661–663). Habits in Yosemite region.

Diagnosis.—Smallest native Salientian in California, head-and-body length less than 50 millimeters (2 inches); all digits with expanded terminal discs; skin smooth, without obvious tubercles; side of head with broad band of dark color through eye, bordered below by narrow stripe of white; body coloration highly variable, ranging

from pale gray through green, brown or red nearly to black; usually marked with broad blotches of darker color in parallel rows on back.

Comparisons.—Distinguished from all other Californian amphibia, save *Hyla arenicolor,* by presence of expanded adhesive discs on tips of all digits and from most species by small size (under 50 millimeters); distinguished from *Hyla arenicolor* by slightly smaller average size, more slender form, wider head, smoother skin on upper surface, presence of dark stripe along side of head, and frequent exhibition of green on body of living animal.

Description.—Form moderate, body depressed, head broad, limbs long; head broadly oval in outline from above, thin in profile, dorsal surface flat, muzzle rounded; external nares nearly terminal, at beginning of indistinct canthus rostralis; internarial width less than interorbital width; upper labial region below canthus rostralis and orbit, slanting outward; anteorbital region slightly longer than orbit; orbit large; interorbital region flat, width three-fourths or more of length of orbit; tympanic membrane nearly round, separated by half or more its width from orbit, greatest diameter not more than one-half length of orbit, overhung by a slight ridge of skin extending backward from orbit; angle of jaw slightly behind posterior margin of orbit; outline of lower jaw nearly semicircular; throat of male with loose wrinkled skin on vocal sac; conspicuous interaxillary fold of skin on breast; free portion of upper arm shorter and more slender than forearm; hand decidedly longer than forearm; palm with one large elongate tubercle at base of inner digit; sesamoid tubercles small; digits long, tips dilated, with little or no webbing between bases, in order of decreasing length, 3, 4, 2, 1; body broad and flat, oval in outline from above; hind limb only slightly stouter than fore limb; femur and tibia about equal in length; tarsus about two-fifths length of foot; two metatarsal tubercles, outer much reduced, inner elongate; sesamoid tubercles small; toes slender, dilated at tips, fourth longest, third and fifth equal, second and first decreasingly shorter; web reduced, margining toes to tips but scalloped deeply to distal end of first (basal) phalanx of fourth toe.

Tongue rounded, moderately thick, greatest width half that of mouth at angles of jaws, broadly attached by anterior two-thirds to floor of mouth; maxillary teeth moderate in size, distributed along whole length of jaw; internal nares round, well up in anterior part of mouth and in from sides of upper jaw; vomerine teeth large, few in number, in two rounded clumps directly between internal nares.

Upper surface generally smooth, or with, at most, scattered, low rounded papillae; sides and ventral surfaces with close-set flat-topped rounded papillae not more than 1 mm. in diameter, largest on sides of body and just posterior to interaxillary fold of skin; plantar surfaces of feet with fine flattened papillae.

Coloration (in life), upper surface highly variable, ranging from yellowish or grayish white through yellow, green and brown of light or dark shade to brownish black; narrow dark stripe along canthus rostralis to orbit and broad dark stripe from posterior margin of orbit to above forearm, constantly present in all color phases; upper lip below dark stripe whitish; ventral surface immaculate, white or pale yellow anteriorly, deeper yellow posteriorly, especially on concealed surfaces of limbs; gular vocal sac of male, blackish.

Description of larva.—Greatest length of head-and-body 17.5 mm.; of tail 30.5 mm.; length of body contained 1.2 to 2.1 in length of tail; external nares about equidistant between end of snout and eyes; internarial width 1.5 to 2.5 in interorbital space; interorbital space 3.1 to 3.7 in length of body; eyes about 25 per cent of body length from tip of snout; spiraculum sinistral, aperture directed backward and upward, center of aperture slightly behind midpoint of body; greatest depth of tail 2.2 to 3.0 in its own length. Eyes on sides of head; dorsal fin originating anterior to upper base of tail; body nearly as wide as high, parallel-sided, rounded behind, greatest width of body behind spiracle.

General coloration above dark yellowish brown, heavily spotted with black; undersurface whitish iridescent with coppery tinges; tail fin mottled with black; muscular part of tail barred with yellow and black; iris golden, divided anteriorly and posteriorly by black.

Labial teeth in $\frac{2}{3}$ rows, first complete, second widely interrupted at middle, third and fourth equal, complete, shorter than first, fifth short, scarcely as long as upper horny jaw; papillae in triple row at sides and double row in center below mouth (fig. GG).

MEASUREMENTS OF ADULT SPECIMENS OF *Hyla regilla* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4884	♀	Sierra Madre, Los Angeles Co.	May 20, 1913	35 3	11.0	11.4	4.0	3.2	7.8	10.0	17.0	17.3	10.5	26
4876	♀	Sierra Madre, Los Angeles Co.	May 20, 1913	39 0	11 0	12 0	3.8	3.4	8 2	11 0	17.3	17.8	11.0	27
4883	♀	Sierra Madre, Los Angeles Co.	May 20, 1913	39.0	12 0	12.5	4.4	3.4	9.3	10.4	18.0	17.4	10.8	29
4453	♀	Sierra Madre, Los Angeles Co.	Apr. 10, 1909	39.3	12.6	13.2	4.0	3.7	9.7	11 2	19.3	19.5	11.0	30
4450	♀	Sierra Madre, Los Angeles Co.	Apr. 10, 1909	41.0	11.7	13 0	4.7	3.4	9 0	10 0	17.0	19.2	11.3	29
4887	♂	Sierra Madre, Los Angeles Co.	May 20, 1913	32.7	9.6	11.2	4.0	2 6	7 5	10 1	14 2	14 5	9.0	22
4449	♂	Sierra Madre, Los Angeles Co.	Apr. 25, 1908	33.5	11.0	11.0	4.5	2.6	7.4	10.0	14.8	15 2	9 2	24
4434	♂	Sierra Madre, Los Angeles Co.	Apr. 11, 1908	34.0	10.3	10 2	3 3	3.3	7.6	9.3	13.5	16.0	10.2	24
4886	♂	Sierra Madre, Los Angeles Co.	May 20, 1913	34.0	10 4	11.2	3 4	3.0	7.3	9.0	14.0	14.5	9.2	23
4451	♂	Sierra Madre, Los Angeles Co.	Apr. 10, 1909	34 8	11.2	11.1	4.0	3 0	7 6	9 6	13.0	15.5	9.1	24
4097	♀	Mill Creek, 2 mi. ne. Tehama, Tehama Co.	June 10, 1912	33.3	10.7	11.4	4.0	3 1	7.3	9.3	14.6	16.5	9.0	24
4096	♀	Mill Creek, 2 mi. ne. Tehama, Tehama Co.	June 9, 1912	34 0	12.3	11.0	4.0	3.3	8 2	10.0	16 2	17.0	10.0	25
5767	♀	Porcupine Flat, Yosemite National Park, 8100 ft.	July 3, 1915	46.5	14.0	16.2	5 0	4 0	10.5	12 2	21.8	22.8	13.7	33
5763	♀	Merced Grove Big Trees, Yosemite National Park 5400 ft.	June 15, 1915	46 6	13.6	16.0	5.0	3.5	11.5	12.3	20.7	22.5	13.5	34
5040	♂	6 mi. n. Willits, Mendocino Co., 1400 ft.	Sept. 1, 1913	34.0	10 0	11 2	4 2	2.5	8 0	9.0	15 2	16.2	9.3	24
4544	♂	2 mi. sw. Napa, Napa Co.	Dec. 16, 1912	36 2	10.8	11.4	4.4	3.1	8.5	9 6	17 4	17 2	10.7	26

History.—This hyla was originally described by Baird and Girard in 1852 on the basis of material collected by the U. S. Exploring Expedition "on Sacramento River, in Oregon and Puget Sound." Additional specimens, collected by the field naturalists of the Pacific Railroad Surveys, and before the wide degree of variation manifested by the species was known, were described by Hallowell, in 1854, as *Hyla scapularis*, *Hyla nebulosa*, and *Hyla scapularis* var. *hypochondriaca*. Cope, in 1866, offered the name *Hyla cadaverina* to replace the name *nebulosa* of Hallowell, which was preoccupied. Cope in 1889 in a general discussion of the species *regilla* mentions three varieties, *scapularis*, *regilla*, and *laticeps*, the latter a new name proposed here to designate specimens from Lower California. Cope here as elsewhere did not apply these varietal names with any regard to geography.

Test, in 1898, after a careful study of 512 specimens of this species from 75 localities (Vancouver Island, B. C., to Cape San Lucas, Lower California, and east to Vegas Valley, Nevada) concluded that all of the foregoing names and including *Hyla curta* Cope (1866*a*) of Lower California should be referred to the single species *regilla*.

Range.—*Hyla regilla* is widely distributed on the Pacific Coast, rivaling *Triturus torosus* in the extent of territory occupied and extending inland much farther than that species. At the north it has been found in British Columbia at "Chilowyuck [=Chilliwack] Lake" (Cope, 1889, p. 360), at Hatzic (Cope, 1893, p. 181; Fannin, 1898, p. 58), San Juan and Sumas Prairies (Boulenger, 1882*a*, p. 374), and on Vancouver Island (Boulenger, *loc. cit.;* Test, 1898, pp. 480, 491). It is common about Puget Sound (Cope, *loc. cit.*). It extends south throughout western Washington, Oregon, and California and has been found in Lower California from Ensenada south to San José del Cabo (Van Denburgh, 1895*a*, p. 557). Inland, at the north, it has been found in Washington, at Springdale, Stevens County (Blanchard, 1921, p. 6), and at Fort Walla Walla (Cope, 1889, p. 361), in Idaho at Payette Lake, Boise County, and Boise, Ada County (Van Denburgh and Slevin, 1921*b*, p. 41), in Oregon at Prineville, Crook County (Mus. Vert. Zool.), and Klamath Falls, Klamath County (Calif. Acad. Sci.), and in Nevada in Virgin Valley and Humboldt County (Mus. Vert. Zool.; Taylor, 1912, pp. 342–343), and in Vegas Valley (Stejneger, 1893, p. 224; Van Denburgh and Slevin, 1921*a*, p. 30).

In California, *Hyla regilla* ranges more widely than any other amphibian, the deserts in the southeastern portion of the State being the only general areas where it does not occur. It is found at sea level in many places along the coast and it ranges up in the Sierra Nevada to, or above, timber line. Some stations of high altitude are the following: Warner Creek at 8000 feet on Lassen Peak, Shasta County (Mus. Vert. Zool.), Mount Conness at 11,600 feet, Yosemite National Park (Grinnell and Storer, 1924, p. 661), south fork of Merced River at 8900 feet (Stejneger, 1893, p. 224), Whitney Meadows, 9800 feet, and Whitney Creek, 10,000 feet or over (Stejneger, 1893, p. 223). It is found locally in several of the mountain ranges east of the Sierra Nevada, as in the Panamint and Charleston ranges at altitudes of from 2600 to 6000 feet (Stejneger, *loc. cit.*).

The easternmost stations of occurrence in southern California are as follows: Johnson Cañon, Panamint Mountains (Stejneger, 1893, p. 223); Shoshone, Inyo County (Mus. Vert. Zool.); Resting Spring, Mohave Desert (Merriam *in* Stejneger, 1893, p. 222); Kern Valley at Weldon (Mus. Vert. Zool.); Fort Tejon (Cope, 1889, p. 360); Antelope Valley near La Liebre Rancho (Stejneger, 1893, p. 224); Oro Grande, San Bernardino County, Bluff Lake, San Bernardino Mountains, Cabezon, Riverside County, Schain's Ranch, San Jacinto Mountains, and Carizzo Creek, eastern San Diego County (specimens in Mus. Vert. Zool.). This species has not been recorded along the east base of the Sierra Nevada and no specimens or records are known from Owens Valley.

Hyla regilla is the only salientian which is found on the islands off the coast of California, having been recorded from Santa Cruz Island (Yarrow and Henshaw, 1878, p. 208; see Van Denburgh, 1905, p. 23), and on Santa Rosa and Santa Catalina islands (Van Denburgh and Slevin, 1914, pp. 135, 137). Off the coast of Lower California it is found on Cerros (or Cedros) Island (Streets, 1877, p. 35; Van Denburgh, 1905, p. 23).

Life-history.—Ecologically as well as geographically, *Hyla regilla* is but slightly restricted. Adults sequester themselves in all sorts of shelters, even at distances of half a mile from water. Growths of water cress or other plants along streams, brush and piles of débris along river banks, burrows of meadow mice and other terrestrial mammals, crevices in boulders, artificial drains and culverts of various sorts, basements of buildings and crevices in outbuildings—all of these

are known locations of occurrence. The same wide range of adaptability is evinced in the matter of spawning places, as indicated beyond.

Hyla regilla seems to have no period of inactivity at the lower altitudes in central California. Individuals are to be seen and the notes of others, coming from various sorts of retreats, are to be heard in every month of the year. More is to be seen and heard of the species during the spawning season, but there seems to be neither hibernation nor aestivation in the valley and foothill regions. Those hylas which live in the mountains must of necessity have a period during the season of low temperatures when they are hidden away in places where they will escape freezing. The extent of this period is unknown for the higher altitudes. In Yosemite Valley on February 28, 1916, when the Valley floor was blanketed with snow to a depth of more than two feet, a chorus of hylas was heard in a snow-rimmed pool near the Merced River. In the Sacramento and San Joaquin valleys, during the heat of the summer hylas are sometimes to be seen in the damp vegetation about pools and stream margins, and the voices of individuals, hidden in safe retreats, are sometimes heard.

This species is by no means a 'tree-toad,' so far as its choice of habitat is concerned. Indeed, it is only seldom that individuals are found in trees, or in other elevated situations. The greater part of the population in California, so far as my personal experience goes, is to be found close to, on, or under, the surface of the ground. In this respect *regilla* differs markedly from *versicolor* of eastern North America and *arborea* of Europe. In the habitats of the latter two species the relative humidity of the atmosphere is high during the summer months, and rains are then of frequent occurrence. The reverse is true in the range of *regilla* save in the humid northwestern coast belt. Death from desiccation would seem to be very much more likely in the dry summer air of interior California. Yet there are a few observations which show that individuals of *regilla* can survive in locations which combine high temperature with at most a very moderate amount of atmospheric moisture. Major Allan Brooks has told the writer of finding individuals of *regilla* during the daytime in the siding of a wooden house exposed to the full heat of the summer sun. They were six feet or more above the ground and in a place where there was no moisture save that in the bodies of the hylas themselves. Mr. Harry J. Snook noted a hyla which regularly spent its days under the edge of a window awning on a house at La Jolla, San Diego County.

The voice of *Hyla regilla* is probably the best known of all amphibian voices in the Pacific states, as it is to be heard in many places and through a long season each year. In the spawning season, or more properly, as long as there is any likelihood of spawning, the 'chorus note,' the note which serves to bring the scattered individuals together for breeding purposes, is uttered. This, to human ears, sounds like *krĕck-ĕk* and is uttered over and over again in rapid sequence. The note is uttered only by the males, and ordinarily only when in, or over, water which is suitable for spawning purposes. I have never heard it given by a female or by a male when out on dry land, although captive individuals in bottles or aquaria will often give it, especially if several are confined together. Normally when 'singing' a male hyla spreads himself out on the surface of the water with all four legs widely extended and this extent of bodily area in combination with the distended vocal sac makes it possible for the animal to float on top of the water with but a minimum of support. Sometimes a croaking hyla will perch on some dead weed or grass stalk close to the surface of the water. When this chorus note is being uttered the single rounded thin-walled vocal sac located on the chin is swelled out to the utmost and serves as a resonator. The sac remains partially distended between notes, reaching its greatest volume at the end of a note, when it is so large as to protrude some distance beyond the end of the snout. When fully relaxed the folded skin on the sac is blackish, but when fully distended all of the black disappears and the surface takes on a slight iridescence.

Individual males watched and timed in the vicinity of Berkeley have been found to utter their notes at about one-second intervals (11, 12, and 15 notes in 15-second intervals, 28 in 30 seconds, another at the rate of 80 a minute and exceptionally even faster). The intervals between notes are very short, just long enough for the air, which has been forced out into the vocal sac, to be returned to the lungs again. An individual hyla may continue in voice for a minute or more without a pause, but usually the 'songs' are shorter.

When several hylas are 'singing' together their individual 'songs' overlap, so that the chorus is continuous. There is a tendency for the notes to be uttered in unison so that at times, when strict synchronism occurs, each alternate note (the main syllable) is stressed. But where there are many hylas together it is difficult to pick out the efforts of the individuals. At times a chorus will continue for many minutes but more often it goes on for a time, then dies out, soon begins again,

and so on. If a person walks out into a marsh where hylas are chorusing the notes quickly cease, ending usually with one or more of the single guttural notes described below. If the intruder remains quiet the hylas will usually resume after a few minutes, one individual beginning in a rather hesitating manner, then being joined by others one by one until the full chorus is under way once more.

In areas of large extent such as the swamps adjacent to some of our main rivers, chorusing hylas may be scattered along for many miles. On the night of April 1, 1923, the writer traveled for several miles along the bank of the San Luis Rey River in San Diego County and all along the route there was such a chorus of hylas that it was impossible to hear any of the other night sounds.

This hyla is to be heard mostly at night, the choruses beginning in the late afternoon and early twilight hours, becoming stronger after full darkness has set in, and gradually dying away in the hours between daybreak and sunrise. However, at the Thornhill pond, near Berkeley, during the months of January to March, hyla choruses were to be heard at almost any hour of the day or night that the pond was visited.

The 'song' season of *Hyla regilla* extends over a long period. As soon as rain pools are formed, in November or December, the males betake themselves to them and thenceforth nightly choruses are to be heard throughout the winter and spring months, up until April, and occasionally even later (for example, May 26, 1921, at Berkeley, and daily until June 9, 1924, at Davis).

At any season of the year this hyla may be heard to utter a single prolonged note, *kr-r-r-ĕck,* lower in pitch than the song note. This note may be used, as indicated above, at the ending of a 'chorus'; but it is also uttered in other seasons of the year when the individuals are hidden in their daytime retreats, and when no 'songs' are to be heard.

The spawning season for *Hyla regilla,* taking its entire range into account, is as long or longer than that of any other species of western amphibian for which life-history data are available. In the lower altitudes of central and southern California spawning commences in January, provided sufficient rain has fallen to establish pools. In the neighborhood of Berkeley spawning extends from early January until the middle of May. The following table lists the available information concerning the spawning of this ubiquitous amphibian.

Locality	Date	Remarks
Strawberry Cañon, Berkeley	Jan. 2, 1922	Eggs found
Thornhill pond, 3 mi. se. Berkeley.	Jan. 4, 1914	4-cell stage to 4 mm. embryos
Thornhill pond	Jan. 5, 1923	Fresh eggs to 5 mm. embryos
Arroyo Seco, Los Angeles [1]	Jan. 9, 1924	Eggs present
Thornhill pond	Jan. 16, 1923	Additional eggs
Thornhill pond	Jan. 20, 1912	Various stages
Arroyo Seco, Los Angeles [1]	Jan. 21, 1923	Eggs present
Thornhill pond	Jan. 25, 1913	Fresh eggs to early embryos
Sierra Madre, Los Angeles Co.[2]	Feb. 1, 1911	4-celled stage
Carmel, Monterey Co.[3]	Feb. 12, ——	Eggs
5 mi. s. Burson, Calaveras Co.	Feb. 15, 1924	7 mm. embryos
Sierra Madre [2]	Feb. 16, 1909	Fresh eggs; hatched Mar. 2
Thornhill pond	Feb. 17, 1922	Early stages to 5 mm. embryos
Thornhill pond	Feb. 18, 1923	Fresh eggs to young larvae
Thornhill pond	Feb. 21, 1922	Fresh eggs
Thornhill pond	Feb. 28, 1922	One fresh mass; few hatched larvae; many embryos
Seattle, Washington [3]	Late February	Eggs
Sierra Madre [2]	Mar. 4, 1911	Eggs
Thornhill pond	Mar. 7, 1922	Fresh eggs
Thornhill pond	Mar. 14, 1922	One fresh egg mass
4 mi. s. Lagrange, Stanislaus Co.	Mar. 14, 1923	Advanced embryos and larvae
Thornhill pond	Mar. 21, 1922	4 mm. embryos; medium sized larvae
Near Escondido, San Diego Co.	Apr. 1, 1923	Eggs in early stages
Sierra Madre	Apr. 4, 1923	Captive female laid during night
Sierra Madre [2]	Apr. 10, 1910	Eggs
Near Felton, Santa Cruz Co.	Apr. 13, 1923	Embryos ready to hatch
Thornhill pond	Apr. 14, 1922	A few large embryos
Baldwin's Lake, Sierra Madre [2].	Apr. 20, 1908	"Swarms" of young just emerging from water
Thornhill pond	May 9, 1922	Larvae 4–12 mm. in head-and-body length; larger ones with all four legs developed
Lafayette, Contra Costa Co.	May 14, 1921	Eggs ready to hatch; some larvae with all four legs developed
Davis, Yolo Co.	May 21, 1924	Newly transformed hylas
Lafayette	May 22, 1921	Fresh eggs and metamorphosed hylas
Sierra Madre [2]	May 24, 1913	One just metamorphosed
Near Monterey, Monterey Co.	May 28, 1921	One recently metamorphosed
Thornhill pond	June 2, 1922	Myriads of young hylas in grass and under weeds near pond; larvae practically all with hind legs

Locality	Date	Remarks
2 mi. s. of Inverness, Marin Co.	July 5, 1919	A newly metamorphosed hyla
Merced Lake, 7,600 feet, Yosemite National Park	July 17, 1921	Larvae up to 37 mm. in total length
Lafayette	July 18, 1922	A few larvae and two recently metamorphosed hylas
San Pablo Hills, e. of El Cerrito, Contra Costa Co.	Aug. 10, 1922	Large larvae and recently metamorphosed hylas

[1] L. H. Miller, MS.
[2] C. L. Camp, MS.
[3] Dickerson, 1906, p. 137.
Except as indicated the data given are from the author's observations.

Mr. Henry W. Henshaw found "vast numbers of the young, in all stages, from the tadpole to the fully developed *Hyla* . . . in a stagnant pool upon Santa Cruz Island" in June, 1875 (Yarrow and Henshaw, 1878, p. 208).

Hyla regilla deposits its eggs in almost any sort of quiet water (pl. 3, fig. 5). The shallow margins of permanent ponds and temporary pools formed in depressions at the sides of roadways are the two most usual locations. Occasionally eggs are deposited at the side of a stream where there is little or no current. In water 75 millimeters or less in depth the egg clusters may be attached to leaves or sticks on the bottom; in deeper water attachment may be made at depths down to 100 millimeters, but most of the masses are found floating on the water surface. The specific gravity of the egg mass is so nearly that of water that a very slight attachment is all that is required to keep the mass from sinking.

The egg clusters of this hyla contain a varying number of eggs. In laboratory aquaria and occasionally in the field single eggs are laid. Some masses total over 60 eggs. Probably the number in a mass reflects in a general way the degree of solitude experienced by a pair when eggs are deposited. Where only one female is laying a few large clumps are to be found. Where many hylas have been spawning in one place the egg masses are small.

At times very large numbers of eggs are laid in a relatively small area. In a small pool near the main Thornhill pond I found, on January 25, 1913, 59 masses in an area approximately 10 by 15 feet. Additional masses were laid in this same area on subsequent nights.

Other areas in this same pond which seemed to be of exactly the same character were not utilized by the species.

The total number of eggs deposited by a single female has been ascertained in two cases. A mated pair was taken from the Thornhill pond on January 31, 1914, and confined in an aquarium. Next morning a total of 730 eggs was found. The average number of eggs in a clump was 18. Another captive which began laying on the night of March 7, 1922, and continued up until 4 P.M. of the day following deposited a total of 1250 eggs; the average of the 58 masses laid was between 21 and 22. The largest mass contained 60 eggs and there were two with the minimum of 9.

The outer jelly coat on the eggs of *Hyla regilla* is a thick soft viscid layer which serves admirably for affixing the eggs to sticks or leaves in the water (pl. 14, fig. 42). In the water this layer expands so that the outlines of the individual eggs are largely obscured. Within this thick soft covering is a thinner but firmer jelly coat which closely surrounds the egg (text fig. Y). When the egg is in the early stages of cleavage this inner coat is spherical; later it becomes drawn out at opposite poles to a lozenge shape. The following table gives measurements of eggs obtained at Thornhill pond in 1922; dimensions are in millimeters:

	Egg	Vitelline capsule	Inner jelly coat	Outer jelly coat
Minimum	1.23	1.29	1.88	4.7
Maximum	1.35	1.41	2 70	6.7

When freshly laid the eggs are light olive brown on the animal pole and white with a very pale yellowish (sometimes greenish) tinge on the vegetative pole.

Most of the eggs of this hyla in the vicinity of Berkeley are spawned at night; when the ponds are visited in the morning it is the usual thing to find the eggs in the 2-cell or 4-cell stage. Development to the stage of hatching, at Berkeley, is accomplished in about two weeks. Eggs spawned on the night of January 31, 1914, and kept in a laboratory where the temperature averaged about 20° C. (68° F.) hatched on February 6.

Newly hatched larvae, within 24 hours of leaving the jelly, measure 6.0 to 7.5 millimeters in total length; the head-and-body length is about 3 millimeters, the greatest height over the fins 1.3 to

1.6 millimeters. Melanophores are scattered over much of the general body surface. The general coloration beneath the pigment is yellow.

For a few days after hatching the larvae are rather quiet but soon thereafter they begin feeding; growth is then quite rapid, the typical blunt compressed body form of the tadpole being assumed within ten days. At the Thornhill pond it was noticed that the *Hyla* larvae were very active and swam up near the surface of the water on bright warm days, whereas in cold, cloudy or rainy weather most of them stayed down near the bottom of the pond and were relatively inactive.

A close check on the subsequent growth of the *Hyla* larva is difficult under field conditions because egg laying continues over a long period. At the Thornhill pond in 1922 the first metamorphosed hylas were noted on May 9. The first eggs in that year were deposited about February 10, so that the egg and larval stages probably involved a period of 88 days. This is more than the time required for *Hyla versicolor* at Ithaca (Wright, 1914, p. 51) and, I believe, is probably longer than is required for *Hyla regilla* in localities in interior California. The Thornhill pond is shaded on the south by a grove of tall Monterey cypresses and other trees, and the locality is often reached by the ocean fogs which cover the San Francisco Bay region, so that the heat quotient of the pond is below that of many of the pools in the warmer parts of the State.

The size attained by this hyla in its larval stage is somewhat variable, depending probably upon the amount of food available, the date upon which egg deposition occurs, and the water temperatures prevailing during larval life. The largest tadpole at hand measures 45 millimeters in total length. One larva only 28 millimeters long has the hind limbs well developed, while another of 40 millimeters has only small limb buds. At metamorphosis the head-and-body length varies from 11.2 to 16.5 millimeters. The foregoing measurements are of specimens obtained at Thornhill pond and at Lafayette.

Transformation, like egg deposition, occurs over a long season. In 1922 the first metamorphosed hylas at Thornhill pond were found on May 9, they were out in numbers on June 2, but as late as August 10 individuals still in process of change were seen there.

The following is a list of recently metamorphosed specimens of *Hyla regilla* from California; it serves to indicate the general seasonal program of the species in different parts of its range.

M. V. Z. No.	Locality	Date	Head-and-body length of recently transformed individuals, in millimeters
4881	Sierra Madre, Los Angeles Co.	May 20, 1913	17
——	Lafayette, Contra Costa Co.	May 22, 1921	15
4562	Sierra Madre, Los Angeles Co.	May 25, 1908	14.8 to 17.3
——	Thornhill pond, 3 mi. se. Berkeley, Alameda Co.	June 2, 1922	11.2 to 12.3
1080	La Puerta, San Diego Co.	June 5, 1909	14.2 to 22.2, possibly the largest were 'yearlings'
4536	Sierra Madre, Los Angeles Co.	June 8, 1908	15.2 to 18
7149	2 mi. s. Lankershim, Los Angeles Co.	June 15, 1918	12.2 to 17.5, two with tail stubs
——	Chain-of-Lakes, Golden Gate Park, San Francisco	July 8, 1923	16 to 19
——	Lafayette, Contra Costa Co.	July 18, 1922	15.5 to 18.0, tail stubs remaining
5042	3 mi. s. Covelo, Mendocino Co.	July 25, 1913	11.4 to 19.5, mostly under 14
7485	T. H. Benton Estate on Butte Creek at 5,000 feet, Siskiyou Co.	Aug. 19, 1920	17.5 to 22.5
6028	1 mi. e. Merced Lake, 7,500 feet, Yosemite National Park.	Aug. 20–23, 1915	13.7 to 17.0
1196	Sherwoods, Mendocino Co.	Aug. 25, 1909	17.0 to 19.6
6203	Hume, 5,300 feet, Fresno Co.	Aug. 21, 1916	16.8 to 18.0

After metamorphosis the young hylas frequent any sort of situations which will provide them with appropriate food and the moisture essential to protect them from desiccation. About permanent ponds and along the banks of streams many of the young frequent the lower bordering vegetation. At the season when the hylas are emerging from the water they find in such surroundings hosts of small soft-bodied insects suitable for food. Considerable growth occurs in the summer and autumn months, as specimens measuring 20.5 to 24.5 millimeters in head-and-body length have been taken in late August and early September. Indeed, slow growth probably continues through the winter months. An individual taken 3 miles south of Davis in Solano County, December 24, 1922, measures 28.2 millimeters in length; several hylas taken at different localities in the State during April, May, and June range from 23.2 to 29 millimeters in total length. Animals approximating the latter dimensions have been observed

about the margin of Thornhill pond during the spring months when spawning was in progress. These are presumably 'yearlings.' They seem to take no part in the breeding activities. The sexually active animals measure from 30 millimeters upward in total length and they are believed to be two years or more in age.

The span of life in *Hyla regilla* is unknown; the largest individuals, over 40 millimeters in length, seem to constitute a size-group above the average of the breeding animals and may therefore represent a class three years (or even more) in age. These large individuals occur sparingly in the general population in various parts of the range although more are at hand from high mountain localities than from the lowlands. Specimens measuring more than 40 millimeters in head-and-body length are in the collection of the Museum of Vertebrate Zoology from the following localities: Oregon, 2 miles south of Barnes, and at Prineville, Crook County; Nevada, Pine Forest Mountains, Humboldt County; California, Warren Peak, Warner Mountains, Modoc County; Porcupine Flat, 8100 feet, and Merced Grove Big Trees, 5400 feet, Yosemite National Park; Allendale, 200 feet, Alameda County; Panamint Mountains, Inyo County; Sierra Madre, 1000 feet, Los Angeles County; and Reche Cañon, 1000 feet, Riverside County.

Food.—Needham (1924, p. 3) examined and reported upon the stomach contents of 18 specimens of *Rana* [= *Hyla*] *regilla* collected in ponds at the head of Laguna Cañon, Orange County, on August 24, 1922. He states:

> To determine what was the food of these tree-frogs, on the 24th of August eighteen specimens were gathered by hand from the tules. Three of these had eaten nothing. The remaining fifteen had eaten a great variety of minute, mostly non-aquatic insects. About 80% of the food consisted about equally of small leaf-hoppers (Jassidae) and small Diptera. The leaf-hoppers were such as abound in shore vegetation. The Diptera were midges, small crane flies and a variety of small Muscoid flies many of which had doubtless developed as larvae in the waters of the pond. The remainder of the food consisted of Myrmecine ants (perhaps 10%), a few parasitic Hymenoptera of the families Ichneumonidae and Braconidae, a few very small beetles, a number of spiders of the genus Erigone and a related genus, and a single terrestrial Isopod crustacean. The insects were all very small, the largest being an Ortalid fly, *Anacampta latiuscula.*

The life-history in relation to the environment.—*Hyla regilla* enjoys a wide dispersal on the Pacific Coast latitudinally and altitudinally. Some members of the species live in the heat of the Mohave Desert, while others live in the glacial environment along the crest of the Sierra Nevada, and many stations of intermediate character are

tenanted by the species. The success of this *Hyla* is due evidently in part to its small size, its long breeding period, its loud voice and the relatively short period of necessarily aquatic existence. By virtue of small size even the adult animals are able to take shelter in narrow crevices where loss of moisture is reduced to a minimum. The long breeding period enables the animals to take advantage of spawning facilities whenever available and however the season in which these facilities may vary from place to place. The loud voice of the male, made possible by the enlarged vocal sac, serves to call all the breeding animals within a wide circle to a suitable spawning place. The males apparently continue in voice as long as there are appropriate facilities. Different breeding places may be available in different years so that there is no tendency toward formation of isolated breeding colonies with consequent development of local races, as with the frogs. A particular *Hyla* may breed in one pond, say to the north of its regular hiding place in one year, while another year the attraction of a chorus in another direction may lead it to join another colony composed of different individuals and pool its hereditary material in a different complex of individuals. This free breeding would tend toward uniformity of stock, such as was found to be the case by Test (1898) in a critical study of the variation in the species.

Rana aurora aurora Baird and Girard. Oregon Red-legged Frog

Rana aurora Baird and Girard (1852*b*, p. 174). Original description, type from Puget Sound [= Washington?].

Rana agilis aurora, Cope (1889, pp. 439–440, text fig. 113), part. General account.

Rana aurora aurora, Camp (1917*b*, p. 124). Critical; range.

Rana aurora aurora, Grinnell and Camp (1917, p. 148, fig. 5). Range in California.

Rana aurora, Stejneger and Barbour (1917, p. 36). General range.

Rana aurora, Boulenger (1920, pp. 448–452). Critical account; range.

Rana aurora aurora, Stejneger and Barbour (1923, p. 34). General range.

Diagnosis.—As for *Rana aurora draytonii* (which see), but greatest size somewhat less (total length up to 76.4 millimeters, 3 inches), dorsal skin smoother and thinner, dorsolateral folds less conspicuous, orbit larger and hind foot proportionately longer.

Comparisons.—See *Rana aurora draytonii.*

Description.—Form moderately stout; head narrowly oval in outline from above, thin in profile; tip of muzzle slanting, overhanging lower jaw; external nares slightly nearer tip of muzzle than orbit, opening dorsally; canthus rostralis distinct, about equal to orbit in length; orbit large; interorbital space flat, about one-half length of

orbit; low ridge on upper jaw, beginning below orbit and extending posteriorly to a rounded papilla above insertion of foreleg; tympanic membrane separated from orbit, nearly round, diameter about two-thirds length of orbit; slight fold of skin extending from posterior side of orbit over tympanic membrane to near insertion of foreleg; lower jaw narrowly oval, truncate at tip; fore limb slender; exposed portion of upper arm shorter than forearm; palm with two parallel tubercles; sesamoid tubercles distinct; digits slender, subequal, in order of decreasing length, 3, 4, 1, 2; sacral hump prominent; dorsolateral folds slight; hind leg much stouter than foreleg; tibia longer than femur; 'heels' overlapping when legs are flexed; tarsus about one-third length of foot; foot slender; two metatarsal tubercles, outer one inconspicuous; sesamoid tubercles large; toes slender, in order of decreasing length, 4, 3, 5, 2, 1; web moderate, scalloped to end of first phalanx on fourth toe.

Tongue narrow, scarcely half width of mouth at angles of jaws, wedge-shaped, posterior end with two lateral lobes, attached by anterior two-thirds to floor of mouth; internal nares small, well behind tip of snout; maxillary teeth large and numerous; vomerine teeth large, few in number, in two separate clusters in broad V-shaped arrangement, between and behind internal nares.

Surfaces of entire animal very smooth everywhere except for slight roughening on ventroposterior portions of femurs.

General coloration (in alcohol) on upper and lateral surfaces dark gray, finely patterned with black; ridge alongside of upper jaw white; tympanic membrane dusky; spot at origin of foreleg and crossbars on fore and hind legs, black; ventral surfaces dull yellow, mottled with dusky.

Live specimens of *aurora* from Seattle, Washington, exhibit the following coloration. Brown, yellowish or olive; small spots or specks of dark brown or black on head, back and sides; space behind eye and including ear, and line below canthus rostralis, black; fold of skin along upper jaw under eye to shoulder, yellowish; upper and lower lips spotted with dark; iris golden yellow; fore limb may be crossed by 3 to 5 narrow dark bands; concealed surfaces yellow and black; throat and undersurface light, obscurely mottled with dark; hand and foot may be purplish gray; much red in coloration on sides of body, on concealed parts of legs and feet, and under arms at insertions (adapted from Dickerson, 1906, p. 216).

Range.—Typical specimens of the present subspecies have been taken in California south to Eureka, Humboldt County. Specimens from Mendocino City, Mendocino County, are intergrades with *draytonii* (Camp, 1917*b*, p. 124). The eastward extent of the range of *aurora* in California is still unknown. In Oregon it has been found at Fort Umpqua (Cope, 1889, p. 440), on Wizard Island in Crater Lake, Klamath County (Evermann, 1897, p. 230), at Eugene, Lane County, and Clear Creek near Oregon City, Clackamas County (Van Denburgh, 1912*b*, p. 159), and at Portland (Pope, MS) and Astoria

(Cope, *loc. cit.*). In Washington it is known from Shoalwater Bay (Cope, *loc. cit.*), Skookumchuck River near Chehalis, Lewis County (Van Denburgh *in* Gilbert and Evermann, 1895, p. 207), Lake Crescent, Clallam County (Meek, 1899, p. 232), and Tacoma, Pierce County (Cope, 1893, p. 181). In British Columbia it has been taken at Hatzic (Cope, 1893, p. 181) and Selkirk Settlement (Yarrow, 1883, p. 176).

MEASUREMENTS OF ADULT SPECIMENS OF *Rana aurora aurora* FROM NORTHWESTERN CALIFORNIA AND OREGON

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
2354[1]	♀	Sept. 1, 1910	57.5	18.7	20.5	7.3	3.5	15.0	18.3	29.0	32.5	17.3	54
5656[2]	♀	May 10, 1916	60.4	19.2	20.3	8.0	4.4	15.2	19.0	30.0	34.5	18.0	54
2317[3]	♀	Aug. 2, 1910	64.3	20.7	23.5	8.6	4.0	16.0	18.8	32.2	35.2	18 7	55
2359[1]	♀	Oct. 8, 1910	74.0	24.0	26.0	8.7	4.6	19.0	20.0	37.0	40.0	22.5	65
5658[2]	♀	May 10, 1916	76.4	24.5	27.5	9.0	4.6	18.5	19.0	37.5	39.6	21.0	62
2358[1]	♂	Oct. 7, 1910	50.6	16.7	16.7	7.0	2.3	14.3	15.0	27.2	28.5	16.4	46
5659[2]	♂	May 10, 1916	53.0	17.7	17.0	7.0	3.5	14.0	15.4	27.0	30.0	16.2	46
5655[2]	♂	May 10, 1916	58.0	18.6	19.0	7.5	3.7	15.2	14.7	26.7	30.6	16.0	48

[1] Arcata, Humboldt Co., Calif.
[2] Reed College, Portland, Oregon.
[3] Eureka, Humboldt Co., Calif.

Rana aurora draytonii Baird and Girard. California Red-legged Frog

(Pl. 3, fig. 5; pl. 4, fig. 7; pl. 6, fig. 12; pl. 12, fig. 35; pl. 15, figs. 45–48; text figs. H, K, L, P, CC, HH)

Rana Draytonii Baird and Girard (1852*b*, p. 174). Original description, type from San Francisco, California.

Rana Lecontii Baird and Girard (1853*a*, pp. 301–302). Type locality, San Francisco, California.

Rana nigricans Hallowell (1854, p. 96). Type locality El Paso Creek, Kern County, California.

Rana draytonii, Girard (1858, pp. 23–25, pl. 2 [figs. 19–24]). General account.

Rana longipes Hallowell (1859, pp. 20–21, pl. 10 [figs. 1*a*–1*c*]). Type locality El Paso Creek, Kern County, California.

Rana Draytonii, Cooper (1868, p. 485). Range.

Rana temporaria aurora, Yarrow and Henshaw (1878, p. 209). Locality records.

Rana lecontii, Boulenger (1882*a*, pp. 42–43). General account.

Rana temporaria aurora, Yarrow (1883, pp. 25, 185), part. General range.
Epirhexis longipes, Yarrow (1883, pp. 24, 176). Locality records.
Rana temporaria aurora, Cope (1883, p. 28). Status.
Rana agilis aurora, Cope (1889, pp. 439–440), part. General account.
Rana draytoni draytoni, Cope (1889, pp. 441–443, pl. 51 [fig. 11], text fig. 114). General account.
Rana draytonii, Stejneger (1893, p. 225). At Monterey.
Rana draytonii, Van Denburgh (1896, p. 1008). Critical; locality records.
Rana aurora, Chamberlain (1897, p. 259; 1898, pp. 255, 259–260), part. Economic status.
Rana aurora draytonii, Camp (1917*b*, p. 124). Range.
Rana draytonii, Stejneger and Barbour (1917, p. 37). General range.
Rana aurora draytonii, Grinnell and Camp (1917, pp. 148–149, fig. 5). Range in California.
Rana draytonii, Boulenger (1920, pp. 446–448). Critical; range.
Rana aurora draytonii, Stephens (1921, p. 60). In San Jacinto Mountains.
Rana aurora draytonii, Stejneger and Barbour (1923, p. 34). General range.
Rana aurora draytonii, Grinnell and Storer (1924, p. 666). In foothills of Yosemite region.

Diagnosis.—Size large, largest of the native frogs in California; head-and-body length up to 114 millimeters ($4\frac{1}{2}$ inches); fold of skin along upper lip light-colored; tympanic membrane smaller in diameter than orbit, not prominently set off from surrounding skin, usually darker in color than rest of head; dorsal skin thick, often roughened with many small papillae; dorsolateral folds conspicuous; hind leg long, when brought forward along side of body inside angle of bent tarsus reaches to or beyond naris; ventral surface of body posteriorly, and hind legs, usually with much red in coloration; vomerine teeth large, in two clusters between internal nares.

Comparisons.—Distinguished from *Scaphiopus* by lack of cutting spade on hind foot and by rounded iris; from all Bufonidae by lack of parotoid gland and presence of dorsolateral folds; from Hylidae by larger size, absence of greatly expanded tips on all toes and presence of dorsolateral folds; from *Rana catesbeiana* by smaller, less conspicuously outlined tympanum, presence of dorsolateral folds, and presence of red in coloration; from *Rana pipiens* by dull light-centered instead of black light-margined dorsal spots, presence of red in coloration, and by larger size of adults; from *Rana pretiosa* by longer hind leg and absence of inky black spots in coloration; from *Rana boylii* by larger vomerine teeth grouped between internal nares, darker tympanic region, presence of light-colored fold along upper lip, presence of conspicuous dorsolateral folds, and presence of red in ventral coloration; from *Rana aurora aurora* by more prominent dorsolateral folds, thicker and rougher skin, larger spots on dorsal surface, and by larger size in full grown adults.

Description (based upon no. 8577, Mus. Vert. Zool., in life).—Form robust, stoutest of the native frogs; head broadly oval in outline from above, thick in profile; end of muzzle acutely rounded; external nares nearer tip of snout than orbit, opening dorsally at side of indistinct

canthus rostralis; orbits prominent; iris wider than high; interorbital space slightly more than half length of orbit; side of head between orbit and margin of jaw, slightly concave; tympanic membrane relatively smooth, oval, slightly higher than wide, separated by half its width from orbit, the surface practically continuous with side of head; narrow ridge from posterior margin of orbit extending obliquely over tympanic membrane to anterior end of dorsolateral fold; broad flattened fold of skin extending backward in line with upper jaw from angle of mouth to above fore limb; fore limb slender; exposed portion of upper arm nearly as long as forearm; hand longer than forearm; palm with two juxtaposed tubercles; digits slender, without webs, rounded at tips, in order of decreasing length, 3, 4, 1, 2; sacral hump prominent; dorsolateral folds passing to either side of hump; hind limb long and of heavy build; femur slightly longer than tibia; hind foot long, nearly one and a half times length of femur; one conspicuous inner metatarsal tubercle; toes long, thickened at base, in order of decreasing length, 4, 3, 5, 2, 1; web extensive, reaching ends of penultimate phalanges except on fourth toe where two phalanges are free.

Tongue narrow, about half width of mouth at angles of jaws, anterior end pointed, general shape cuneiform, posterior end with two narrow lobes, attached by anterior two-thirds to floor of mouth; internal nares well behind tip of snout, and widely separated; vomerine teeth large, in two conspicuous clusters between internal nares; maxillary teeth large and closely spaced.

Fore part of head smooth; entire dorsal surface of body behind orbits, including sides of body below dorsolateral folds and exposed surfaces of hind limbs, with small rounded rough papillae 1 to 2 mm. in diameter; midventral surface of body smooth; under surface of femur areolated; buttocks rugose.

General ground color of upper surface buffy brown to olive brown, somewhat darker posteriorly; ground color of fore part of head ecru-olive, palest along posterior margin of upper jaw, the whole with slight bronzy iridescence; margin of jaw, in narrow line between nostril and eye, and lower border of ridge running backward from orbit, dusky; pupils black, iris black with scattered xanthophores of colonial buff; narrow line along fore and hind margin of iris, colonial buff; tympanum grape green and dusky in irregular pattern, sharply set off in color from surrounding skin which contains much dragon's blood red; dorsolateral folds ecru-olive, slightly differentiated in color from rest of back; back and sides of body with blackish spots, each with a light bronzy central papilla, these smallest and palest anteriorly, larger (up to 5 mm. in diameter) and more conspicuous near urostyle; exposed surface of fore limb, ecru-olive; large spot at junction of forearm and body, another on outside of 'elbow,' a third midway of forearm, and others inside of elbow and near forefoot, black; ground color of undersurface of body, white, mottled with dusky; sides of body and undersurfaces of hind legs between dusky mottlings, dragon's blood red; dorsal surface of hind foot, inner surface of crus, and thigh (except outermost surface), marked with dragon's blood red.

Description of larva.—Greatest length of head-and-body 28 mm.; of tail 55 mm.; length of body contained 1.2 to 2.2 times in length of tail; external nares about equidistant between end of snout and eyes; distance between nares 1.2 to 1.9 in interorbital space; interorbital space 3.4 to 5.2 in length of head-and-body; eyes about 25 per cent of head-and-body length from tip of snout; spiraculum sinistral, the aperture directed backward and slightly upward, center of aperture slightly behind midpoint of head-and-body; anus dextral; greatest depth of tail 2.5 to 3.2 in its own length. General coloration of upper and lateral surfaces of body dark brownish (not greenish), much mottled and with numerous dark spots 1 to 2 mm. in diameter, these having diffuse edges; middle of belly whitish iridescent, with slight pinkish tinge; chin and throat region and sides of under surface finely mottled with light and blackish markings with a slight iridescence; tail lighter than body, with blackish markings separating myomeres and with a light mottled pattern on caudal crests; iris dull bronzy yellow.

Labial teeth in $\frac{2}{3}$ rows; uppermost complete, second divided, each short and the two separated by width of lower jaw; third of full width interrupted medially; fourth complete but slightly shortened laterally; fifth shorter than fourth; three rows of papillae on each side of mouth region, one row complete across lower border (fig. HH).

MEASUREMENTS OF ADULT SPECIMENS OF *Rana aurora draytonii* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4411	♀	Santa Anita Cañon, Los Angeles Co.	Apr. 10, 1909	94.3	33 0	36 5	10.5	6 3	26.3	27 0	49 0	51 0	26.5	74.5
7150	♀	Thornhill pond, 3 mi. se. Berkeley	Feb. 18, 1919	96 0	34 0	37.0	11.0	5 0	25.5	28 0	52 0	53.2	30 0	67.0
5612	♀	[near] Berkeley, Alameda Co.	Mar. 29, 1916	96.3	32 3	38 0	11.2	5 4	25 0	28 2	56.7	53 6	29.8	82.0
4409	♀	Sierra Madre, Los Angeles Co.	Apr. 10, 1909	97.0	34.0	35 2	11 2	6.9	25.8	26.0	52 2	52.7	26.8	76.0
4402	♀	Sierra Madre, Los Angeles Co.	Apr. 25, 1908	106.0	37.4	39 0	12.0	7 5	26.8	31.0	58 2	55.2	31.0	81.0
8577	♀	Dublin, Alameda Co.	May —, 1922	114.0	39.0	43.0	13.4	7.2	27.0	27.5	66.0	63.0	35.0	93.0
7151	♂	Thornhill pond, 3 mi. se. Berkeley	Feb. 18, 1919	78.5	28.0	27.5	10.0	3.5	22.0	22.0	40.0	44.0	24.0	55.0
6111	♂	Michigan Bluff, Placer Co.	Aug. 12, 1916	81 5	27.0	29.0	10 2	7.3	22.0	21.5	44 0	47.0	25 0	58.5
4401	♂	Sierra Madre, Los Angeles Co.	Apr. 20, 1908	82.0	28.1	30 5	9.7	5.0	21.7	22.0	40 6	44 0	23.3	69.0
4404	♂	Sierra Madre, Los Angeles Co.	Apr. 25, 1908	84.0	28.6	28.6	9.4	4.0	19.5	22.0	39 7	42 1	22.3	65.0

Remarks on coloration.—The general tone of coloration is quite variable in the individuals of this species. *Rana aurora draytonii* alone among our California frogs (Ranidae) possesses considerable power of color change. This change can be rapidly effected, and once

accomplished the result can be maintained for a long period of time. The large adult which furnished the basis for the preceding color description, while in the laboratory maintained the 'light phase' just described, and this whether exposed to daylight in a glass-walled terrarium or in a practically light-tight box. Previously this particular individual had been kept in a fish pond in the water of which there was an abundance of black peaty material. In that situation the frog was quite blackish, that is it was in the 'dark phase.' Once, in the laboratory, when suddenly seized in the hand and taken out of its terrarium, the frog 'turned black.' The color change was effected in a few seconds of time. The change was particularly noticeable on the ventral surface, where the red and white areas were largely obscured by the spreading of the black pigment.

Young frogs, just after metamorphosis, are marked with a golden iridescence on the dorsolateral folds.

History.—*Rana aurora draytonii* was first described by Baird and Girard in 1852 from specimens collected by the United States Exploring Expedition at, or near, San Francisco. The following year it was redescribed as *Rana Lecontii* by the same authors, and Hallowell later described frogs of the same species from El Paso Creek, Kern County, as *Rana nigricans* and *Rana longipes*. The relationships of *draytonii* have been variously interpreted, but it is now known to be a conspicuous southern form of the *aurora* stock, which is found along the Pacific Coast from southern British Columbia to northern Lower California.

Range.—*Rana aurora draytonii* is found chiefly in California. Camp (1917*b*, p. 124) draws the line between the subspecies *aurora* and *draytonii* at Mendocino City, Mendocino County; typical *draytonii* extends northward to Gualala, Mendocino County (Camp, *loc. cit.*), to 3 miles west of the summit of Mount Sanhedrin, Mendocino County (Mus. Vert. Zool.); and to Michigan Bluff, Placer County (Grinnell and Camp, 1917, p. 149). Easterly it ranges to Redding, Shasta County (specimen in Calif. Acad. Sci.), and into the foothills of the Sierra Nevada at Michigan Bluff (as above), at Smith Creek, 6 miles east of Coulterville, Mariposa County, at Snelling, Merced County (Mus. Vert. Zool.), and at El Paso Creek, Kern County (Hallowell, 1854, p. 96). In southern California it occurs along the base of the San Gabriel and adjacent mountain ranges, as above Altadena (Storer, MS), at Sierra Madre (Camp, MS; specimens in Mus. Vert. Zool.), at Colton (Van Denburgh, 1896, p. 1008), and at Riverside (Van Denburgh, 1912*a*, p. 149). In San Diego County it has

been taken at Campo (Grinnell and Camp, *loc. cit.*); in northern Lower California it has been found on San Pedro Martir Mountain (Van Denburgh, *loc. cit.*), and at San Tomas, La Grulla, and Rancho San Antonio (Schmidt, 1922, p. 634). Boulenger (1920, pp. 446–448) records a specimen from Tia Juana, the California Academy of Sciences has a specimen from Victorville, San Bernardino County, and there is in the Museum of Vertebrate Zoology a specimen from Oro Grande (Halleck Postoffice), San Bernardino County, on the Mohave Desert. Whether these specimens represent natural occurrences or whether they are 'transplants' for 'frog farming' is unknown.

In the San Joaquin Valley *draytonii* has been found at Gadwell, Merced County, and Minkler, Fresno County (Mus. Vert. Zool.). No records are known for the Sacramento Valley. In the Coast Ranges it is present in many localities from Santa Barbara north to the stations listed above. Altitudinally this frog ranges from sea level as at Monterey (Stejneger, 1893, p. 225), to 4000 feet in the mountains of southern California (Camp, 1917*b*, p. 124).

Knowledge of the local distribution of this frog is much less complete than for some of the other species of western amphibians, due to the fact that the adults are quite wary, often escaping the attention of collectors, and to the further fact that the species is more active by night than by day and may not be seen unless especially hunted for after nightfall. This species has been used on several 'frog farms' in California; but in no authenticated case which has come to the writer's attention has it been transplanted to areas outside the natural range of the species.

Life-history.—This is essentially a pond-dwelling frog. It may occur along stream courses, but only in places where there are large permanent pools. The larval period is relatively long and the adult frogs are highly aquatic, spending practically all of their time in the water; situations in which the pools become reduced or dry up completely are not likely to be inhabited by the species. It is known to occur in a number of water-storage reservoirs and other artificial ponds, and it has been cultivated with some degree of success in ponds of quiet water on one or more 'frog farms' within the State. Camp (MS) states that it has been found in water tunnels near Sierra Madre and occasionally under dripping ledges and overhanging rocks on the borders of foothill streams. However, it is not to be found out on bare rocks in streams, as is commonly the case with *Rana boylii.*

To illustrate the nature of the habitat of this species the following exact places of occurrence which have come to the attention of the writer may be mentioned. (1) Pool at base of small waterfall in Eaton Cañon northeast of Pasadena; (2) small permanent reservoirs in shade of trees on orange ranches near Sierra Madre: (3) pools on course of creek in the Arroyo Seco between Los Angeles and Pasadena; (4) permanent artificial reservoir in hills southeast of Berkeley; (5) pools on fresh-water marshes west of Point Reyes Station, Marin County; (6) quiet water of slough adjacent to Merced River at Snelling.

Adults of *draytonii* may sometimes be seen out in the daytime, as in the pools on the marshes of Olema Creek, mentioned above. The animals there rested on the mat of aquatic vegetation which covered the surface of the water, ordinarily with only their heads above the surface. At the first hint of danger, such as the approach of a person, they dove, one by one, into the depths of the pools and remained below for many minutes.

The habits of *draytonii* during the winter months vary according to locality. In the vicinity of Berkeley individuals have been seen out as late as November 20, and spawning has occurred as early as February 6. The finding of fresh eggs at Los Angeles as early as January 9 (1924) argues for but a brief season of inactivity during the winter season in that locality. Camp (MS) states that but few of these frogs can be found during the winter months at Sierra Madre (altitude 1200 feet); he once found several buried deep in wet leaves in December. However, January 9, 1910, is a date of record for eggs at Sierra Madre (Camp, MS). At Sampson Flats, 7 miles north of Dunlap, Fresno County (altitude about 2000 feet), on January 13, 1924, Mr. Joseph Dixon (MS) found seven individuals of *draytonii* which were evidently wintering in a layer of silt in the bottom of a boxed-in spring, the water being about 12 inches deep and the silt 6 inches. The frogs were entirely hidden from view and were torpid when taken out. The ground adjacent to the spring remained frozen through the day and there were patches of snow nearby.

In general, the ponds and creek pools which are the haunts of this species are seldom frozen, and if they do freeze, the ice seldom lasts for more than part of one day. In the lowland range of the species the percentage of nights with freezing temperatures is very small. At the moderate altitudes occupied by the species along the western flank of the Sierra Nevada and along the southern flank of the Sierra

San Gabriel a slightly longer season of inactivity is indicated. But *draytonii* goes through nothing like the real winter hibernation which the ranas of eastern North America experience.

The call of this frog is a series of low tremulous or 'gurgling' notes, resembling somewhat the notes uttered by *Rana boylii.* The notes may be given when a captive frog is held in the hand, especially during the breeding season. Camp (MS) states that when seized suddenly and roughly, *draytonii* will sometimes open its mouth widely and deliver a "piercing human-like scream." The same observer reports that frogs of this species were heard 'croaking' in November, 1909.

Draytonii is one of the earliest amphibians to spawn in California. In the neighborhood of Berkeley it is third in the sequence of the aquatic species, being preceded by *Triturus torosus* and *Hyla regilla.* In the neighborhood of Los Angeles it precedes one if not both of those species. Most of the data on life-history presented below have been obtained from observations at a pond situated in the hills about 3 miles southeast of Berkeley near Thornhill station on the San Francisco-Sacramento Railroad. This pond is known to local naturalists as "Lone Willow Pond," but throughout the present paper is designated as "Thornhill Pond" (pl. 3, fig. 5). The pond is an artificial one, and, according to Dr. A. M. Meads (MS), the red-legged frog was 'planted' there a number of years ago by H. O. Medau who then conducted a frog farm at the place.

Data for spawning are as follows:

March 24, 1917, embryos about 4 mm. long (P. E. Smith, MS).
February 18, 1919, 1 mass, jelly not yet swollen to normal size.
February 6, 1921, 3 masses; eggs in early stages of cleavage.
February 21, 1922, 9 masses; eggs unsegmented or in early stages of cleavage.
February 18, 1923, 1 mass; eggs in morula stage.

In the Arroyo Seco, opposite Avenue 66, in the Highland Park district of Los Angeles, Dr. Loye H. Miller found an egg mass of this species on January 21, 1923, which already contained elongated embryos; other egg masses in early stages of cleavage were found there on January 28, 1923; in 1924, eggs in the two-cell stage were found in the same place on January 9. Camp (MS) states that in the vicinity of Sierra Madre, Los Angeles County, the months of January and February seem to mark the height of the breeding season. January 9, 1910, is a date of record there. He also states that eggs were laid by

this species in the same locality in November, 1909. Upon turning to the Weather Bureau records, I find that a heavy rainfall, of 2.91 inches, was recorded for Sierra Madre in November, 1909, whereas the average for November is only 1.66 inches.

So far as my information goes, *draytonii* spawns only at night. I have never found any adult frogs on their spawning grounds during the daytime, and the generally reclusive habits of the species at other times of the year would suggest nocturnal spawning. Egg masses found by nine o'clock in the morning are usually in the earliest stages of cleavage. At the Thornhill pond the masses always have been deposited in a shallow overflow area at the western end, which is flooded only during the late winter and early spring. During the summer months this area is completely dry and covered with a heavy stand of tall dock and of milk thistle. About the first of the calendar year, in winters of average rainfall, the pond water rises and overflows this area, and in February the frogs resort to this place for spawning purposes. *Spirogyra* and other green algae have become abundant in the water and there is a considerable growth of duckweed (*Lemna* sp.). The grasses are then just starting.

The eggs in this location have been deposited in water from 75 to 150 millimeters in depth, usually in situations where upon extrusion they became attached to dead weed stalks and were supported at the surface (pl. 15, fig. 48). The specific gravity of a complete egg mass is slightly greater than that of the water, so that some sort of attachment is necessary to keep the egg mass near the surface of the water.

On February 6, 1921, three egg masses were found in this shallow area. In 1922 visits were paid to the pond at frequent intervals, but it was not until the morning of February 21 that egg masses were found. On this date, nine masses laid evidently on the nights of February 19 and 20 were discovered within a circle not more than 12 meters (40 feet) in diameter. Each mass was separated from its nearest neighbors by 60 centimeters or more. Other egg masses were laid in the week following, one or more on the night of February 27; a visit on March 7 showed that one more mass had been deposited during the intervening week. No more fresh masses were found after that date. On February 18, 1923, a single egg mass of this species was found in the same general location. It had probably been laid on the night of February 16. A visit to the pond on March 5 failed to show any additional egg masses.

The jelly surrounding the individual eggs when freshly laid has a blue hyaline tint which is lost or becomes obscured as development proceeds. The jelly is soft to touch yet viscid, and it is difficult to separate individual eggs from the general mass. The approximate outside dimensions, in millimeters, of eight of the masses observed on February 21 were as follows:

65 × 100 × 75	150 × 100 × 100	100 × 75 × 75
125 × 75 × 75	100 × 150 × 75	125 × 75 × 75
150 × 100 × 75	125 × 100 × 65	

One egg mass collected February 6, 1921, had a volume of 1530 cc. One hundred eggs were found to have a volume of 53 cc., and the approximate number of eggs in the mass was therefore 2886 eggs. An actual count of another mass yielded 2250 embryos and infertile eggs. The mass collected February 18, 1923, had a total displacement of 1180 cc., and a sample containing 417 eggs displaced 130 cc. of water. This would mean 3785 eggs in the mass (pl. 15, fig. 48). The seeming discrepancy between the figures for the first and third masses is explained by the fact that in the latter many of the eggs lacked the outermost jelly envelope which contributes largely to the bulk of the individual egg and hence to the mass. The large size of the sample used would seem to correct any error from this source. It seems safe to say that the egg masses of *draytonii* contain from 2000 to 3500 or 4000 eggs.

The general mass is like that of other ranas in that the jelly coverings of the individual eggs are evident on the surface of the mass. The individual eggs are black, heavily pigmented on the animal pole, and white at the vegetable pole, there being some variation in the amount of the white showing on different eggs. Each egg is enclosed in three spherical 'jelly' envelopes which can be readily distinguished even with the unaided eye (fig. CC). Measurement of a number of eggs from the 1922 material gave the following results (in millimeters):

	Egg	Vitelline capsule	Inner jelly coat	Middle jelly coat	Outer jelly coat
Minimum	2.06	2.28	3.10	3.94	7.55
Maximum	2.30	2.46	4.00	4.93	9.10
Average of 9	2.19	2.35	3.59	4.45	8.46

Four eggs from one of the 1921 masses were somewhat larger:

	Egg	Vitelline capsule	Inner jelly coat	Middle jelly coat	Outer jelly coat
Minimum	2.50	2.84	4.50	5.50	9.70
Maximum	2.81	2.95	5.00	6.40	11.80

The exact rate of development is unknown. A few measurements of air and water temperatures at the Thornhill Pond are as follows:

Date (1922)	Hour	Water temperature		Air temperature	
February 3	Morning	Pond lightly frozen		——	——
February 9	4:30 p.m.	10.0° C.	50° F.	11.2° C.	52° F.
February 17	4:00 p.m.	11.0	51.8	13.5	56.3
February 21	9:00 a.m.	8.8	47.9	8.8	47.9
February 28	9:00 a.m.	5.5 to 7.5	41.9–45.5	11.0	51.8
March 7	9:30 a.m.	9.0	48.2	12.0 to 13.0	53.6–55.4
March 21	9:00 a.m.	11.5	52.7	9.5	49.1

Despite the rather low temperatures indicated, the eggs laid on February 19 and 20 contained embryos about 3 millimeters long by March 7, which had already hatched out of the jelly by March 14.

At hatching, the larvae are sooty brown in color and measure 8.8 to 10.3 millimeters in total length. The adhesive discs, stomodaeum, dextral anus, and two external gill filaments on each side are distinct at hatching. In one mass which was kept in the laboratory it was noted that prior to hatching the jelly coat in which the embryo was then contained was about 5 millimeters in diameter. Only two jelly coats could then be distinguished, so the innermost one may have become dissolved, affording the embryo greater space for development.

For some time after hatching the larvae rest on the surface of the jelly, which becomes gradually softer and softer and eventually disappears. There were larvae on the jelly masses in the Thornhill pond up to March 27, but by April 14 tadpoles of several sizes were generally distributed in the shallower parts of the pond. Upon April 19 hind limb buds were detected on some of the tadpoles. Thereafter, due to the drying of the shallower waters at the west end of the pond, the larvae which survived by escaping into the main body of the pond were more difficult to find. Several large individuals were seen on June 9, the largest of those collected being 68 millimeters in total length. A two-hour search of the pond on August 10, when the aquatic vegetation was exceedingly dense, revealed only one large

tadpole of this species which, unfortunately, escaped capture. The time at which the larvae in this pond metamorphose into frogs is unknown. Mr. D. A. Jones reports finding young frogs there on November 20, 1922, but these in all probability had transformed at some time earlier. The history of the frogs in the Thornhill pond unfortunately ends here.

Observations in other localities make it possible to piece out the life-history. *Draytonii* occurs in numbers on the fresh-water marshes just west of Point Reyes Station, Marin County, where Olema Creek flows down to the southern end of Tomales Bay. Young frogs of this species which had evidently transformed from tadpoles of the current season's growth were seen in numbers in the fresh-water pools of the marsh on August 26, 1922. No larvae were observed on this date although no careful search was made for them. A visit to the same marshes on May 5, 1923, revealed many larvae, of various sizes up to a total length of 83 millimeters; but no young frogs which could be ascribed to the 1923 crop of tadpoles were seen. One of these larvae kept in an aquarium at Berkeley completed its metamorphosis about June 15, while others were still typical larvae on that date.

In the Arroyo Seco, Los Angeles, opposite Avenue 66, Mr. Alden Miller at my request collected samples of the *draytonii* population of larvae during the spring of 1923. Part of these were taken from the same pool which contained hatching larvae on January 21, and all were taken within a quarter-mile of that pool. The following table gives the measurements of this material, as made by the writer.

Date (1923)	Total length in millimeters			Remarks
	Minimum	Maximum	Average of ten largest	
April 7	24	56	50.6	Smallest not sought for; hind limb buds just appearing
April 15	14	58		
April 22	23	58		
April 29	26	62		
May 6	22	71	65.6	One completely metamorphosed, head-and-body length 30 mm.
May 13	22	72	62.7	
May 27	46	72	67.0	
June 13	36	75	69.2	
June 20	45	80	73.0	Several metamorphosing, others with hind legs well developed; head-and-body length 25 to 28 mm.

This table indicates the general size of the tadpole population, but it does not necessarily portray the seasonal programs of individual larvae. Thus metamorphosis had already occurred in one case by May 6; increasing numbers of metamorphosed individuals were probably removed from the population after that date. The general tadpole population, however, continued to increase in size up to June 20 when most of the larvae were well on the way toward metamorphosis.

Camp (MS) notes the finding of very large tadpoles, presumably of this species, in a reservoir near Sierra Madre on April 10, 1909. He states that tadpoles of this species are likely to be seen at almost every season of the year and he thinks it probable that in some places they take more than one year to arrive at the stage of transformation. From the evidence available in other localities I think that usually but part of one season is required for development from egg to frog, though exceptional instances might occur where the tadpoles would winter over and metamorphose the following spring.

The size at metamorphosis in *draytonii* is only slightly larger than in *boylii*. Two specimens of the former from the Arroyo Seco, Los Angeles, collected May 15, 1921, are 27 millimeters in head-and-body length. In one of these the tail was nearly resorbed, a short stump about 3 millimeters long being all that remained. The other specimen was just beginning to transform and had a total length, from nose to end of tail, of 72 millimeters. A third specimen, on which the fore limbs had not yet burst through the opercular membrane, measured about 74 millimeters in length over all. These specimens were measured after being in formalin solution for two years. One larva collected on the Olema Creek marshes, Marin County, May 6, 1923, before preservation, measured 83 millimeters in total length. On the basis of size (age) groups it seems probable that *Rana aurora draytonii* begins breeding activities in its third year.

The two species of tadpoles which by reason of large size and general similarity of appearance are likely to be confused in California are those of the native *Rana aurora draytonii* and the introduced *Rana catesbeiana*. The ecologic preferences of the two are similar. *Draytonii* ordinarily accomplishes in one season (5 to 7 months) a degree of growth which takes two full years in *catesbeiana*, although the latter, prior to metamorphosis, reaches greater size than any examples of *draytonii* which have come to hand. Close comparison, side by side, of living examples of these two species, each of about

83 millimeters total length and with hind limb buds in evidence (third stage larvae of Dugés), shows the following important differences:

	Rana aurora draytonii	*Rana catesbeiana*
	Larva from pond in marshes at south end of Tomales Bay, Marin County, California.	Larva from creek pool near Farmington, San Joaquin County, California.
Snout	More pointed in outline as viewed from above.	More rounded in outline.
Eyes	Rather close together.	Farther separated.
Body	Broadest posterior to spiraculum, ended behind abruptly.	Broadest anterior to spiraculum, tapering behind gradually into tail.
Tail	Greatest height posterior to midpoint, bluntly tapered toward end.	Greatest height anterior to midpoint, sharply tapered toward end.
	Broader at base as viewed from above.	Narrower at base as viewed from above.
Coloration	Ground color of dorsal and lateral surfaces of body, dark browns and yellows.	Ground color of dorsal and lateral surfaces of body, olive green of light or dark tone.
Spots on body	Diffuse margined, more than 1 mm. in diameter.	Sharp-margined, not over 1 mm. in diameter.
Under surface	Center of belly with *pinkish iridescence*, margins mixed iridescent and blackish in fine pattern.	Center of belly whitish, *not iridescent*, margins mottled with dark pattern of large size.
Tail	Mottled with light spots.	With small dark dots as on dorsal surface of body.

The life-history in relation to the environment.—*Rana aurora draytonii* shows less special adaptation to the climatic conditions of the Pacific Coast than many of the other species of western amphibians. It seeks and remains in situations where the water supply is permanent and therefore has no need to develop special adaptive responses to the semi-arid climate. Its local occurrence is limited to those places in which there are permanent pools either natural or artificial. General dispersal over the country probably occurred at some time in the past when conditions were less arid. Some spreading probably occurs during unusually wet winters, but the rate of such dispersal must be slow at best. *Draytonii* spawns very early in the year, on the average in January and February, with extreme limits

in November and March. Occupying as it does, permanent bodies of water, there is no need to delay spawning operations to a late date in the spring, as is the case with the stream frog (*Rana boylii*).

Temperature seems to have little to do with the initiation of spawning activities, as there is no conspicuous alteration in temperature coincident with egg deposition so far as data available to the author indicate. The only correlation which has occurred to the writer is that of maximum filling of ponds, a feature upon which, unfortunately, no measurements are available. In the one pond (Thornhill) which has been under observation for the life-history of *draytonii*, the time of egg deposition corresponds roughly with that of high water. The occurrence of spawning in November at Sierra Madre in a month of unusually heavy rainfall is a further indication that the filling of the ponds may be an important factor. Eggs deposited at the highest stage of the pond are then unlikely to be submerged (and covered with pond vegetation), but are, on the other hand, constantly exposed to the heat of the sun and thus develop at a maximum rate. Subsequent to hatching, the larvae of *draytonii* inhabit the shallow water adjacent to the main pond, so long as such shallows are inundated. The quick growths of grass or aquatic vegetation which occur in such places soon provide shelter for the tadpoles, and the more rapid warming of the shallow layer of water each day hastens growth of the diatoms and green algae upon which the tadpoles feed. Metamorphosis is evidently accomplished by late spring to midsummer (May–July), giving the young animals whose food requirements have changed from vegetable to animal material an opportunity to forage and grow to somewhat larger size in preparation for tiding over the winter season when food is scarce.

Rana boylii boylii Baird. California Yellow-legged Frog

(Pl. 3, fig. 6; pl. 12, fig. 34; pl. 16, figs. 49 [upper right], 50; text figs. AA, II, PP)

Rana boylii Baird (1854, p. 62). Original description, type from [Eldorado County] California.
Rana boylii, Baird (1859*b*, p. 12).
Rana Boylii, Cooper (1868, p. 485). Range.
Rana pretiosa, Yarrow and Henshaw (1878, p. 210), part. Locality records.
Rana pretiosa, Yarrow (1883, pp. 25, 186), part. Locality record.
Rana pachyderma Cope (1883, pp. 25–26). Type locality, U. S. Fish Hatchery, McCloud River, Shasta County, California.
Rana boylii, Cope (1889, pp. 444–447, text fig. 115). General account.
Rana boylii, Boulenger (1892, p. 453).
Rana boylii, Stejneger (1893, pp. 226–227). Critical; locality records.

Rana boylii, Dickerson (1906, pp. 221–222, pl. 2 [fig. 7], pl. 84 [figs. 264–266]). General account.
Rana boylii, Van Denburgh (1912*b*, p. 159). Occurrence in Oregon.
Rana boylii boylii, Camp (1917*b*, pp. 117–118, fig. 3). Critical; locality records.
Rana boylii boylii, Grinnell and Camp (1917, p. 146, fig. 5). Range in California.
Rana boylii boylii, Stejneger and Barbour, 1917, p., 36; 1923, p. 34). General range.
Rana boylii, Boulenger (1920, pp. 469–471), part. Critical; locality records.
Rana boylii boylii, Storer (1923, p. 8). In Coast Range.
Rana boylii boylii, Grinnell and Storer (1924, pp. 663–665). In foothills of Yosemite region.

Diagnosis.—Size small, head-and-body length up to 66 millimeters (2⅝ inches); dorsal surface of body roughened with many fine pointed papillae; vomerine teeth small, scattered on two elongate ridges between internal nares; tympanic membrane like rest of head; upper labial region without raised white ridge; red not present in coloration of ventral surface; hind leg long, inside angle of bent tarsus reaching at least to nares and usually beyond; each eyelid with light patch anteriorly and dark patch posteriorly.

Comparisons.—Distinguished from *Scaphiopus* by lack of cutting spade on hind foot and rounded instead of vertically elliptical pupil; from Bufonidae by absence of parotoid glands, and by presence of teeth in jaws; from Hylidae, by larger size, lesser expansion of digits at tips and absence of dark stripe on side of head; from *Rana aurora* ssp., and *Rana pretiosa* ssp., by rudimentary vomerine teeth, roughened tympanic membrane, absence of light stripe along upper lip, and (usually) absence of conspicuous dorsolateral folds; from *Rana catesbeiana* by smaller adult size, much smaller and less conspicuous tympanic membrane, and rougher dorsal surface; from *Rana pipiens* by broader form of body, rudimentary vomerine teeth, smaller and roughened tympanic membrane, absence of dorsolateral folds and presence of roughened body skin with ill-defined dark markings; from *Rana boylii muscosa* by presence of light patch in front of dark area on upper eyelid, by darker general coloration, and less expanded tips of toes; from *Rana boylii sierrae* by longer hind legs, greater width of head, rougher tympanic membrane, absence of dorsolateral folds, and presence of light patch on upper eyelid. (Compare pl. 12, figs. 34, 36; pl. 17, fig. 51 [left].)

Description.—Form stout, body broad, limbs short; head broad yet pointed, oval in outline from above, thick in profile, muzzle descending, rounded at tip; external nares not terminal but nearer tip of snout than orbit; internarial width greater than interorbital width; canthus rostralis distinct, beginning at nostril, its length shorter than that of orbit; orbit large; interorbital space about two-thirds length of orbit; tympanic membrane rounded, smaller than, and separated slightly from, orbit, depressed below adjacent surface of head; angle of jaw under tympanic membrane; lower jaw oval in outline; fore limb stout; free portion of upper arm shorter than forearm; hand longer than forearm; fingers rather stout, blunt-ended, third longest,

remaining three nearly equal (3, 1, 2); sesamoid tubercles rounded; palmar tubercles inconspicuous or lacking; body thick; sacral hump moderately conspicuous; hind limb short and stocky; tibia slightly longer than femur; tarsus slightly more than one-third length of foot; two metatarsal tubercles, inner one much the larger and elongate; sesamoid tubercle conspicuous, rounded or oval; toes blunt, with tips slightly expanded; web large, only slightly scalloped.

Tongue large, practically filling floor of mouth, oval in outline, bluntly rounded anteriorly, two rather long lobes posteriorly, attached by anterior half to floor of mouth; maxillary teeth small and numerous along entire length of upper jaw; internal nares small, widely separated, close to sides of upper jaw; vomerine teeth small, on two convergent ridges between and slightly behind internal nares.

Exposed dorsal and lateral surfaces of body and limbs roughened with numerous fine papillae, each ending in a fine point; surfaces of head, margin of upper jaw, and tympanic membrane, roughened like rest of body; palm smooth; lower surface of hind foot roughened; ventral surface of head and body and concealed surfaces of limbs, smooth; ventroposterior surface of femur with numerous flat-topped rounded areolae.

General coloration above, dark grayish or yellowish brown, marked with irregular blotches of blackish; limbs crossed by bars of blackish, wider and more numerous on hind limb than on fore limb; ventral surface white, pale yellow on posterior part of body and hind limbs; throat, sides of body, and anterior surface of femur, mottled with blackish.

Description of larva.—Greatest length of head-and-body, 18 millimeters; of tail 29 mm.; length of head-and-body contained 1.2 to 1.8 times in length of tail; external nares midway between tip of snout and orbit; eyes well up on top of head; interorbital space 5 to 9 times in length of head-and-body; spiraculum sinistral, aperture directed backward and upward, center of aperture decidedly behind midpoint of body; anus dextral; greatest depth of tail (over fins) 3.3 to 4.2 in its own length; height of muscular portion of tail 4.2 to 6 in head-and-body length.

Labial teeth in 7/5 rows, first complete across entire mouth region, second to seventh inclusive interrupted medially, the successive rows progressively shorter and shorter; eighth row shorter than first, and interrupted medially, ninth to twelfth complete, successively shorter; papillae in single row on lateral and ventral borders of mouth region (fig. II).

An example of *Rana boylii boylii,* with all four legs fully developed but with tail not yet resorbed, which was collected in San Pablo Creek, Contra Costa County, on August 7, 1922, was colored as follows:

Ground color of back deep olive, paling posteriorly and laterally through citrine drab, and becoming dark olive buff on exposed surfaces of legs; a dark V-shaped patch of dusky across middle of upper eyelid and interorbital space; snout and side of upper jaw mottled with brownish black; back and sides with scattered spots of blackish, each about 2 mm. in diameter and each with a central light dot of wood brown; exposed surface of legs and toes with crossbars of brownish black; upper part of tail citrine drab, lower half olive buff; whole

surface of tail mottled with 2 mm. spots of blackish; chin white, slightly clouded; under surface of body between legs, white; under surfaces of legs dirty white.

MEASUREMENTS OF ADULT SPECIMENS OF *Rana boylii boylii* FROM CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
6110[1]	♀	Fyffe, Eldorado Co., 3600 ft.	July 31, 1916	48.8	16.0	18.5	5.7	5 5	11.0	12 2	...	28.5	14.3	38.0
5961	♀	Sweetwater Creek, Mariposa Co., 3800 ft.	Nov. 1, 1915	54 0	17 2	21.2	6.8	4 0	13 0	15.0	29.5	32.5	15.5	46.0
6109[1]	♀	Fyffe, Eldorado Co., 3600 ft.	July 31, 1916	57 0	18 2	22 5	6 4	3 8	13.0	16.0	31.7	33.0	16.0	47.0
5686	♀	3 mi. ne. Coulterville, Mariposa Co., 3200 ft.	June 3, 1915	62 7	19.2	23.3	7 0	5 2	16 0	14 3	30.3	34 7	17.8	47.0
6339	♀	Muir Woods, Marin Co.	Sept. 30, 1917	66.0	20.6	26 5	8 0	4.6	15 8	16 8	35 0	37.3	18.0	51.0
2410	♂	Muir Woods, Marin Co.	Sept. 9, 1910	39 0	14 0	15 0	5.4	4 4	10 0	11.1	21.2	21.8	11.2	31 0
2409	♂	Muir Woods, Marin Co.	Mar. 5, 1910	45 5	14.7	18 1	5.7	3 3	11.1	12 7	24 0	25.4	12.6	36.0
5080	♂	3 mi. s. Covelo, Mendocino Co.	July 23, 1913	48 7	16.5	20.4	5 6	3 0	10.8	13.6	27.5	27.8	14.0	40.0
8514	♂	Frank Valley, Marin Co.	May 1, 1922	51.0	14.7	17 2	6 6	......	13 8	12 2	26.4	29.0	14.0	41.0
4084	♂	w. side Mt. Diablo, Contra Costa Co., 2750 ft.	July 22, 1912	54.0	15 7	20 1	7 0	4.0	13 3	13.7	30.7	28 8	14.0	42.5

[1] Near topotypes.

History.—*Rana boylii* was originally described by Baird in 1854 from "California," on the basis (Cope, 1889, p. 447) of two specimens obtained in Eldorado County by Dr. C. C. Boyle. In earlier years this frog was confused with a northern form, *pretiosa,* and Boulenger (1892), probably on the basis of inadequate material, confused *boylii* with *draytonii.* Cope in 1883 described material from the McCloud River as *Rana pachyderma.* Stejneger in 1893 (pp. 225–227) pointed out the confusion which had existed then for many years concerning the western frogs; but it was not until 1917 that Camp, using the extensive series collected by the Museum of Vertebrate Zoology, and with adequate knowledge of the differing habitats of the several species, indicated the proper relationships of the western forms and described the three well-marked varieties of *boylii.*

Range.—The *boylii* group of frogs is restricted to California and southern Oregon. Individuals of this species have been found in Douglas County, Oregon, at Drain (specimens in Calif. Acad. Sci.) and at Roseburg (Van Denburgh, 1912*b*, p. 159). Cope (1889, p. 447) mentions specimens from Ashland, Jackson County. The subspecific status of these is undetermined, but presumably they all belong to

Rana boylii boylii. In California this subspecies inhabits the foothill districts of the State south to Bodfish, Kern County (Camp, 1917*b*, p. 118). In the Coast Ranges it has been found commonly south to central Monterey County (Storer, 1923, p. 8) and may range to Santa Barbara (Cope, 1889, p. 434, specimen no. 8679). Easterly in the Coast Ranges it comes close to the margin of the Sacramento-San Joaquin Valley as in Putah Cañon, 4 miles west of Winters, Yolo County (Storer, MS), near Vacaville, Solano County, near Mount Diablo, Contra Costa County, Corral Hollow, San Joaquin County, and in the foothills 22 miles southwest of Los Baños, Merced County (Camp, *loc. cit.*). In the northern Sacramento Valley it has been found in Mill Creek near Tehama, Tehama County (Camp, *loc. cit.*). Along the western flank of the Sierra Nevada it occurs in the foothill streams up to the margin of the Transition Zone, as at Fyffe, Eldorado County (3600 feet), Sweetwater Creek, Mariposa County (3800 feet), and Hume, Fresno County (5300 feet) (Mus. Vert. Zool.). Its southernmost station of record is Kern River near Bodfish (Camp, *loc. cit.*). This form reaches through Kern Gap, as at Fay Creek (4100 feet), 6 miles north of Weldon, Kern County, and has been found on the east slope of the Sierra Nevada at Mono Lake (Camp, *loc. cit.*). Frogs of the *boylii* group have been recorded from the vicinity of Lake Tahoe (Boulenger, 1920, pp. 469–471), but as that author 'lumps' the three subspecies of this group the subspecific identity remains to be determined.

Boylii occurs in the Transition Zone of the Coast Ranges from Mendocino County south at least to Santa Clara County ("Palo Alto" [Boulenger, *loc. cit.*]), and is very common in many of the creeks in that zone north of San Francisco Bay. In the Sierra Nevada it is restricted to the Upper Sonoran Zone, reaching but a short distance into the Transition, as at Fyffe and Hume. It has not been recorded at good mid-Transition Zone localities there. On the other hand, it is not now known to occur out in the Lower Sonoran Zone of the San Joaquin Valley. There seems to be a hiatus in the range of the species *boylii* in the mountains at the southern end of the San Joaquin Valley; at least the intensive collecting which has been carried on in the vicinity of old Fort Tejon has failed to reveal the presence of any stream frogs between Bodfish, Kern County, where *R. b. boylii* occurs, and Little Rock Creek, on the northern slope of the San Gabriel Mountains, Los Angeles County, where the southern subspecies, *muscosa*, is found.

Life-history.—*Rana boylii boylii* is strictly a stream-inhabiting frog. The whole life of an individual is passed along a stream, and the seasonal life-cycle is closely correlated with the annual cycle of the stream. The adult frogs of this species spend much of their time perched on rocks in the stream or on the bank, but in the latter place they never go more than two or three feet from the margin of the water. If approached, even from the direction of the stream, they invariably seek safety by leaping into the water, and immediately swim with swift strokes down to the bottom. In streams with silt on the bottom they hide in the mud and silt which their movements stir up; in clear waters they take refuge under overhanging rocks. The obscure pattern of markings on the back and sides of this frog and the roughened surface of the skin blend well with most of the backgrounds against which the animals are apt to be seen, either above or below the surface of the water, and this constitutes a factor of safety, at least so far as human eyes are concerned.

It seems doubtful if *Rana boylii boylii* has any period of real hibernation such as is annually experienced by the frogs in the northeastern states. The winter season in the foothill districts of California is very mild. There are very few days upon which the temperature drops below 32° F. Only exceptionally does the ground freeze and then only for short periods and the depth to which the freezing penetrates is but slight. The creeks are never frozen, save occasionally at the surface. The mean minimum monthly temperature (text fig. B) in the range of *Rana boylii boylii* does not drop below 36° F. There is consequently no need for a hibernating period. The only actual fact which bears in any way on the point is the finding of two specimens of this species beneath rocks in the creek bed of Claremont (Telegraph) Cañon near Berkeley on November 17, 1912. These two frogs were not torpid. Evidence from the winter activity of other local species of amphibians suggests that there is no need for hibernation on the part of this species. Furthermore, the conditions which obtain along many of the streams inhabited by *Rana boylii boylii* are, during the winter months, such as would be distinctly adverse to hibernation by a stream-inhabiting amphibian. The courses of many of the California foothill streams are rocky, with but little mud in the stream bed. The winter and early spring time, from November until March, when frogs in the east are in hibernation, is, in California, ordinarily a period when the streams are swollen with rain water and actively engaged, by reason of their increased rate of flow, in the transport of

relatively heavy sediments. Any accumulations of mud which might occur in the creek beds would then be likely to be washed out, and any frogs in them would have their places of hibernation destroyed.

Frogs which live in regions experiencing a prolonged low winter temperature hibernate to avoid being frozen and also because at that season the forms of insect and invertebrate life upon which they depend for food are scarce or entirely unavailable. Conditions in the California foothill country are quite different: There is little or no danger to the frogs from freezing, and some insects are active during the winter season.

Specimens of *Rana boylii boylii* have been captured or seen abroad at several lowland stations on the dates given below, which suggests that if there is any period of inactivity it must be extremely short. The fact that few collectors have been at work in the midwinter period is a factor which must be considered in this connection.

EXTREME SEASONAL DATES OF CAPTURE FOR *Rana boylii boylii* IN CALIFORNIA

Locality	Date of capture	Authority
Sweetwater Creek (3,800 feet), Mariposa Co.	Nov. 1, 1915	M. V. Z. no. 5961
Cañon, near Monticello, Napa Co.	Nov. 12, 1923	Storer, MS.
Claremont Cañon, near Berkeley, Alameda Co.	Nov. 17, 1912	M. V. Z. nos. 4393–94
Fairfax, Marin Co.	Feb. 2, 1913	M. V. Z. nos. 4734–38
Putah Cañon, 4 mi. w. of Winters, Yolo Co.	Feb. 3, 1924	Storer, MS.
Muir Woods, Marin Co.	Mar. 5, 1910	M. V. Z. no. 2408
San Pablo Creek near Orinda, Contra Costa Co.	Mar. 14, 1922	Storer, MS.
Corral Hollow, sw. of Tracy, San Joaquin Co.	Mar. 14, 1911	M. V. Z. no. 2566

However these frogs may spend the 'winter' period, it is obvious, from field experience, that the adults are active for several weeks before the advent of the breeding period. In the vicinity of San Francisco Bay the spawning season extends from the latter part of March to the first of May. No data are at hand for the season in the Sierra Nevada. In the heart of the Transition Zone of the north coast counties, for example in the redwood belt of Mendocino County, the season is later. The exact time of spawning there is unknown, but late in June, 1922, I was unable to find either eggs or larvae.

The table following gives data on the spawning of *boylii* in central California. The localities mentioned are mostly in the Upper Sonoran

Zone. Frank Valley and Papermill Creek are on the boundary between the Transition and Upper Sonoran zones. In most of the instances of spawning given in the table the frogs were collected in the field and taken to the laboratory, where they spawned one or more days later. In these cases the dates given are those of the day following the night during which eggs were laid, save in a few cases expressly indicated otherwise. For the data pertaining to the years from 1916 to 1921 I am indebted to Dr. P. E. Smith, of the Department of Anatomy, University of California, who has collected *Rana boylii* for use in his experimental work on the hypophysis (P. E. Smith, 1920). Mr. Frank Bassett supplied the material dated April 21, 1922.

Spawning Dates of *Rana boylii boylii* in Central California

Locality from which frogs were obtained or where eggs were found in stream	Date	Remarks
San Pablo Creek, Contra Costa Co.	Apr. 1, 1913	
Frank Valley, Marin Co.	Apr. 14, 1916	
San Pablo Creek, Contra Costa Co.	Apr. 17, 1916	
Laurel Dell, Marin Co.	Mar. 28, 1917 and until Apr. 9, 1917	
Frank Valley, Marin Co.	Apr. 22, 24, and 25, 1917	
Niles Cañon, Alameda Co.	Prior to Apr. 3, 1918	
Niles Cañon, Alameda Co.	Apr. 20, 1918	Last eggs here laid on this date
San Pablo Creek, Contra Costa Co.	Prior to Apr. 15, 1919	
San Pablo Creek, Contra Costa Co.	Apr. 17 and 19, 1919	
Niles Cañon, Alameda Co.	Apr. 22, 1919	Nine egg masses found in the creek in various stages
Frank Valley, Marin Co.	Apr. 5, 9, 13, and 29, 1921	
Frank Valley, Marin Co.	Apr. 10, 1922	
Isabel Creek (near entrance of Long Branch), Mount Hamilton, Santa Clara Co.	Apr. 21, 1922	
Frank Valley, Marin Co.	May 1, 1922	Eight masses in the creek in various stages of development
San Pablo Creek, near Orinda, Contra Costa Co.	Apr. 20, 1923	Two masses in the creek, started in development
Papermill Creek, near Tocaloma, Marin Co.	May 5, 1923	About 25 masses in the creek, some recently laid, some with development under way, some hatching; one 'ripe' female

The egg masses of *Rana boylii* are deposited in the water of the same streams which the adult animals inhabit throughout the year. The egg masses are usually placed in the shallow water toward the margins of the streams. In Frank Valley, Marin County, where the spawning habits of this species were observed in detail on May 1, 1922, egg masses were found in water not over 125 millimeters in depth. All were attached to the sides of stones in the stream bed, one on the up-stream side of the stone, the others on the downstream surfaces. The jelly of the protecting coats on masses deposited in the stream soon becomes coated with sediment. A striking similarity in color thus develops between the sediment-covered egg jelly and the brownish colored growths of the alga *Nostoc*, which are present on the rocks in the stream at the season when the eggs of *Rana boylii* are in the water. While this covering of sediment might be thought to have some protective value in disguising the egg masses so that they would escape the attention of birds which might otherwise discover and feed upon the eggs, the (brownish) sediment to some extent prevents access of heat rays from the sun, and thus would seem to act to delay development. The egg masses are swayed by the current and it seems probable that a high degree of oxygenation results from such movement and from the constant passage of fresh stream water over the jelly coats. With the 'ripe' adults which have been held captive in a cement-lined outdoor aquarium in the Department of Anatomy on the University campus, the egg masses are almost invariably attached to the rough side walls of the enclosure. Each mass in the wild probably represents the entire laying of one female, as is usually true in other species of the genus *Rana*.

The egg mass is typically raniform, like a compact cluster of grapes, with the capsules of individual eggs showing distinctly on the surface of the mass (pl. 16, fig. 50). The eggs mass of *boylii* is very much smaller than that of *draytonii* or of *catesbeiana*, and as compared with the former is somewhat firmer in texture. Two representative masses collected in Frank Valley, Marin County, on May 1, 1922, measured approximately 50 by 50 by 30 millimeters and 60 by 90 by 50 millimeters in outside dimensions. The following table gives the weight, and approximate volume and dimensions, of eight masses, from Papermill Creek, Marin County, collected May 5, 1923. Development had commenced but in some had not proceeded very far.

MEASUREMENTS OF EGG MASSES OF *Rana boylii boylii* COLLECTED IN PAPERMILL CREEK, MARIN COUNTY, CALIFORNIA, ON MAY 5, 1923

Weight in grams	Approximate volume in cubic centimeters	Approximate outside dimensions in millimeters
33	30	75 x 45 x 30
30	28	45 x 30 x 35
39.5	35	65 x 40 x 30
57 (embryos well formed)	65	65 x 50 x 35
21	15	55 x 30 x 25
47	55	45 x 45 x 45
42	40	55 x 45 x 35
48	45	40 x 45 x 45

Three of the masses listed above were placed in strong formalin, with the result that the individual eggs were separated one from another. Counts of these masses yielded the following totals: 919, 952, and 1037.

The individual eggs are black above, with a small area of clear white at the vegetative pole. There are three distinct jelly coats around each egg (text fig. AA). The dimensions of the egg and its coverings (in millimeters) are as follows:

	Egg	Vitelline capsule	Inner jelly coat	Middle jelly coat	Outer jelly coat
Minimum	1.93	1.98	2.32	2.58	3.88
Maximum	2.48	2.53	2.94	3.35	4.47
Average of 8	2.21	2.26	2.51	2.85	4.08

Development had already started in some of these eggs; fresh eggs might be found to measure slightly less than the maxima given above, and the averages would be slightly smaller.

The time of development in the stream waters is not known. It probably varies according to the exact location of the eggs in the stream, depending upon whether they are placed in a situation where the full effect of the sun is received throughout the day or in a place shaded during the morning or afternoon hours. Another variable is introduced in the difference in the weather with its effect upon the general temperature of the stream water. No data have been found giving the seasonal heat quotient of western foothill streams. One lot of eggs kept in the laboratory at a temperature ranging from about

60° to 65° F. began hatching on the twelfth day, and the greater part of the larvae were out on the thirteenth day.

Freshly hatched larvae measure as follows: total length, 7.3 to 7.7 mm.; tip of snout to gills, 1.47 mm.; height of fin over all at the anus 1.87 mm. In the field the young, upon emerging from the jelly mass, are found clinging to or lying upon the latter in the first few days after hatching.

Subsequent to hatching, the tadpoles of *Rana boylii boylii* experience a fairly rapid growth, considering the nature of their habitat. From three to four months seems to be required for the growth between hatching and metamorphosis.

The earliest record of transformation is from a creek at Lafayette, Contra Costa County, where larvae undergoing metamorphosis were found on July 18, 1922. At the immediate locality of capture of the specimens this creek is in the bottom of a gulch about 20 feet in depth. The concentration of heat due to the protected location of this particular part of the creek may have been responsible for the early arrival at metamorphosis. The same year (1922) in an adjacent stream (San Pablo Creek) eggs were found on April 20, 1923, and by August 7, the greater part of the *boylii* population there had already metamorphosed. Transformed young frogs were found in Pine Cañon, near Mount Diablo, July 22, 1912. Larvae of *Rana boylii boylii* seen in a creek at Manor, Marin County, on July 6, 1919, measured 40 millimeters or less in total length, and hind limbs were developed on some individuals. Two larvae from near Vacaville, Solano County, collected July 3, 1912, are 28 millimeters in total length. In Papermill Creek, where eggs were found in abundance on May 5, 1923, I found, on July 8, 1922, only scattered larvae of small size. In 1922, it was not until August 26 that the larvae in this creek were undergoing metamorphosis.

The larvae of *Rana boylii boylii* gain hind limb buds when about 30 millimeters in total length. At metamorphosis the younger frogs of this species are comparatively large (pl. 16, fig. 49). Several specimens acually undergoing the transformation, which were collected in San Pablo Creek on August 7, 1922, measured 22.0 to 23.6 millimeters in head-and-body length and one was 26 millimeters long. Several fully metamorphosed young frogs collected at the same time ranged from 23.2 to 30 millimeters in head-and-body length. The young frogs seem to make very little progress in growth during the winter season following their metamorphosis. Young animals col-

lected in the creeks in the spring of the following season show practically no increase in size. Thus, five young collected in Papermill Creek near Tocaloma, Marin County, on May 5, 1923, measure only 22.7 to 26.1 millimeters in head-and-body length. These figures are to be compared with those just mentioned, of animals taken August 7, 1922. Growth evidently begins with the advent of warm weather, as four specimens collected along this same creek on July 9, 1922, measured from 31.5 to 38.5 millimeters in head-and-body length.

The tadpole of *Rana boylii boylii,* while not grossly different from the larvae of other California Salientia, presents a peculiarity in the form and number of the 'teeth' which line the region about the mouth. There are *seven* rows above the mouth and *five* below and the series below the lower lip are on a rather loose flap of skin which permits of more than the ordinary amount of movement. Of the teeth superior to the mouth only the topmost row is complete, the others are divided, and each successive row becomes shorter until the seventh is but a short lateral row on each side of the mouth proper, each half containing but a very few teeth. The five ventral rows all extend across the 'lower lip.'

The form of mouthparts in the present species is strongly suggestive of that of the larva of *Ascaphus truei* as described by Gaige (1920). *Ascaphus* has 13 rows of teeth, three above and ten below the mouth, while *Rana boylii* has twelve rows with seven above and five below. Mrs. Gaige states (p. 6) that the tadpoles of *Ascaphus* "cling with the mouth to the stones in the creeks." *Boylii* has not been observed to do this in the case of specimens collected in central California. It may be a mere coincidence that these two Salientian larvae are provided with such an elaborate series of larval teeth, but it seems significant that such development has appeared only in those two species in this order which have become restricted completely to life in flowing streams, even though the two species belong to separate suborders.

A generous sample of the *boylii* population from any one locality on a particular date usually reveals frogs of two distinct sizes, some under 40 millimeters and others ranging from 50 to 70 millimeters in head-and-body length. I take this to mean that at least two years are required for growth to adult size. The 'yearlings,' which constitute the smaller size group, take no part in breeding activities. Some of the frogs in the 'adult' category are, for this species, large and 'pachydermous' and thus give the appearance of being decidedly aged.

It may be that a certain limited percentage of the population lives on for a period beyond two years. In general, however, the environment of this species, as indicated below, is ill suited to the continuance of large individuals or of any over a period of years.

The food of *boylii* has not been investigated in detail. One individual collected near Covelo, Mendocino County, on July 19, 1913, was found to have its stomach crammed with grasshoppers. *Boylii,* in being active by day along stream courses, is probably able to make use of both aquatic and terrestrial insects, and it is probably able to get some provender at night as well.

The life-history in relation to the environment.—*Rana boylii boylii,* the stream frog of central California, stands as a type distinct in habitat among the frogs of northern North America. Only its close southern relative (*R. b. muscosa*) displays the same restriction of habitat. A parallel case is found with the 'tree-toad' of the southwest, *Hyla arenicolor.*

As might be expected, the fortunes of the *boylii* population fluctuate with those of the stream. In its life-history *boylii* exhibits several striking specializations which are in all probability related to the requirements of life of a stream-dwelling species.

Instead of the winter being the critical season in the life of this frog, it would seem that the summer months hold greater possibilities of danger for *Rana boylii boylii.* To explain the basis for this presumption it will be necessary to discuss in some detail the annual cycle of a typical California foothill stream.

In the first place, the greater amount of the rainfall in the foothill country comes during the late winter and early spring months. A lesser amount falls during the late spring and practically none during the summer season (see text fig. D). The slopes which form the drainage basin of a foothill stream are usually ill suited to retaining any great amount of the rainfall. The surface cover is chiefly of the dwarf forest or chaparral, with little or no leafy débris on the ground to serve as a spongy absorbent to hold the water as it falls. Consequently the run-off is extremely rapid; a heavy rain is followed immediately by the swelling of the stream and much material is washed down the slopes and carried into the creek. At the end of the rainy season the stream rapidly subsides, and for a short period there is a moderate flow of clear water. The water, however, quickly lessens in amount, the stream becomes a series of pools connected by shallow

riffles, and often by summer (July and August) all but the very largest and deepest pools disappear.

To illustrate graphically the seasonal cycle of a foothill stream, recourse has been had to the records of stream measurements which have been made during the past two decades by the United States Geological Survey. The amount of water passing in many of the streams where measurements have been made is of course greater than in the small creeks inhabited by the bulk of the *boylii* population. Yet the seasonal history of the larger and smaller streams is probably much the same save perhaps for the midsummer dry or low-water period.

The stream chosen for study is Arroyo Seco Creek on the east slope of the Santa Lucia Mountains in Monterey County. This creek, although of considerable size, is known to be inhabited by *Rana boylii boylii* (Storer, 1923, p. 8), the record of water measurements for the creek is complete over a considerable period, and the stream is unmodified by man either by diversions or dams at, or above, the place at which the measurements here used were taken. The data used therefore give the normal behavior of such a creek under the variations to be met with in a ten-year seasonal cycle of climatic conditions in California. The drainage basin of this stream is moderate in extent (215 square miles). Arroyo Seco Creek heads in the Santa Lucia Mountains where a small amount of snow falls during the winter months. The lower portion of the drainage basin lies in the foothill-chaparral region.

The complete and principal graph (text fig. PP) shows the average daily discharge of water in second-feet during the decade, 1909–1918. The two shorter graphs show, respectively, the maximum and minimum discharges during the season in which the spawning and larval development in *boylii* is carried on. The record of daily discharge in second-feet was chosen rather than the gage-height because the former exhibits more strikingly the violent changes in amount of run-off which follow precipitation in the drainage basin. For convenience in plotting, only the readings on the first, seventh, thirteenth, nineteenth, and twenty-fifth days of each month were used. The great extent to which such a stream may be swollen as a result of heavy rains over the drainage area is indicated by the maximum discharges recorded for certain dates in the years included in the record. These are as follows:

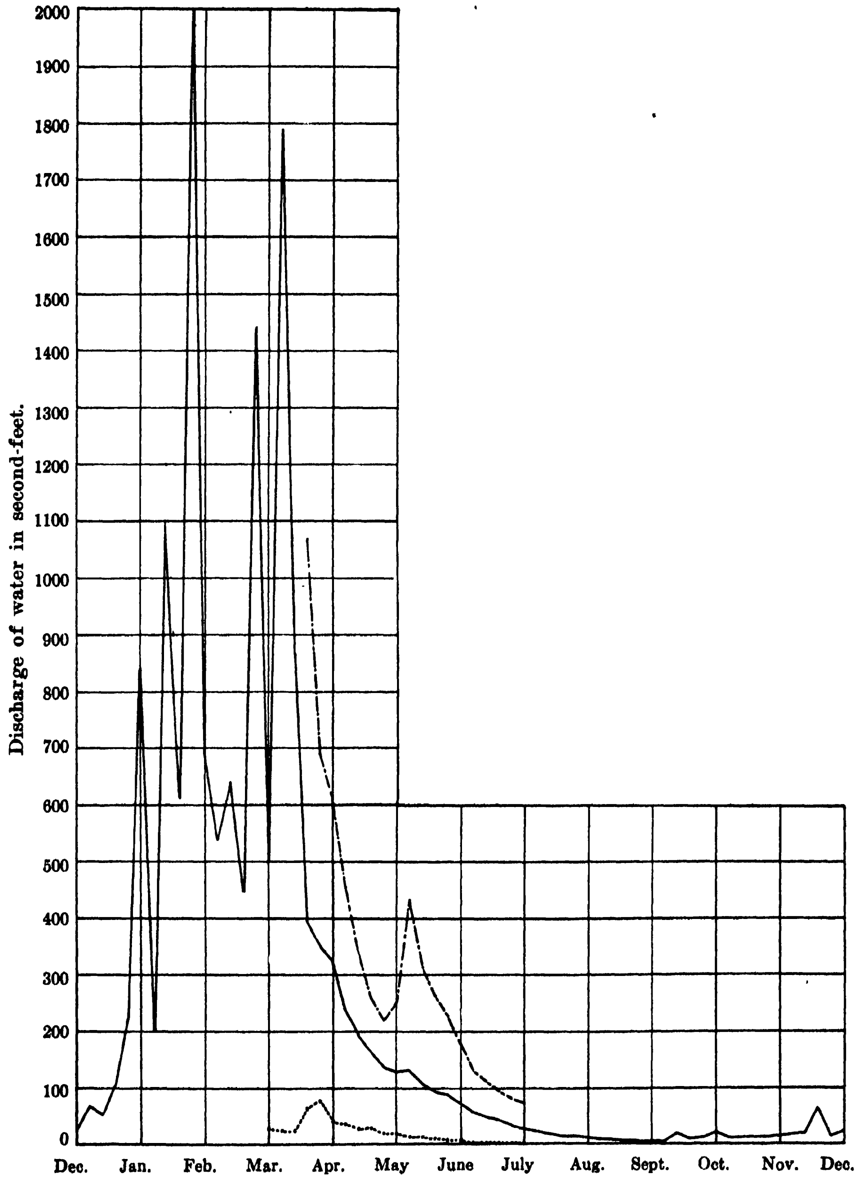


Fig. PP. Graph showing seasonal history of a California foothill stream, the habitat of *Rana boylii boylii*. Complete graph shows average discharge of water in second-feet in Arroyo Seco Creek, 15 miles south of Soledad, Monterey County, California, throughout the year, for the period 1909–1918; upper partial graph shows maximum flow during portion of year when *Rana boylii boylii* is spawning, lower partial graph minimum flow during same season. Compiled from data in U. S. Geological Survey, Water Supply Papers nos. 271, 291, 311, 331, 361, 391, 411, 441, 461, 481.

		Maximum discharge in second-feet
1909	January 1	6,150
1910	March 21	1,780
1911	January 29	5,910
1912	March 12	1,080
1913	January 15	925
1916	January 17	18,800
1917	February 21	11,300
1918	March 12	6,200

According to the notes accompanying the report for 1913 (the driest year in the decade upon which the graph is based) there was, through that season, water in pools along the course of the creek even when no flow could be recorded by the gage. Such pools would of course serve as places of refuge for *boylii.* It will be noted that the peak of high water is, *on the average,* reached in March. By April first the stream is decreasing in volume and only exceptionally does it rise after that date (maximum of May 7, 1915). Even in an unusually dry year (such as 1913) there is a small flow of water in the stream during the spring months and this water lasts until mid-July.

The temperature of the water in many of these foothill streams during earlier months of the year is not unduly low and would not be inimical to the eggs of *boylii.* The adults are easily able to withstand such temperature, as is indicated by their activity in March and earlier when the streams are still swift and turbid. But eggs deposited during the period of rapid and turbid flow would be likely to be washed downstream or else would fail to receive any great quantity of heat from the sunlight. Should eggs be deposited and hatch during this period of rapid-flowing turbid water, the larvae, especially when in the inactive stage immediately following hatching, would be washed downstream or killed by being buried in sediment. On the other hand, if the larval period should continue into the early autumn months there would be great danger that many of the larvae would fail to complete their growth and metamorphosis prior to the drying up of the stream. There is then but a brief period, from April, when the water has become clear and the current slow, until early July or August, when the stream begins to dry up, during which *boylii* can deposit its eggs with the likelihood that they will hatch and the larvae pass successfully through the metamorphosis. And this is exactly the period during which we find the eggs and tadpoles of this frog.

During the brief period in which the stream runs clear the water is often warmed by the sun to a considerable degree where the stream is shallow and lacks a close border of trees. Such warming of course also raises the temperature and increases the rate of development in egg masses or larvae resting on the stream bottom.

The drying up of the creek in summer constitutes the greatest menace to an amphibian such as *boylii*. As the stream becomes slowly restricted, there is a gradual concentration of the frogs in the pools. When these become shallow a large number of the individuals fall easy prey to raccoons and herons and other species of animals which feed upon frogs. The few frogs which escape probably do so by taking refuge in the deeper permanent pools, or perhaps in crevices in the bank; and the small size of the adults may be a response to the need of being able to take shelter in small holes available in such places. But observation is needed on this latter point.

It is also probable that, as a creek dries up progressively from the lower reaches toward the headwaters, the frogs tend to move up the stream course as is indicated in the case of *Hyla arenicolor*.

The presence of *boylii* in the streams of the Transition Zone of the northern Coast Ranges and its apparent absence in the streams in this zone in the Sierra Nevada are probably due to the seasonal differences in behavior of the streams in the two regions. In the humid portions of the Coast Ranges the stream grades are, in general, low, and the slopes of the drainage basins are covered with large amounts of humus and vegetational growth. When rain falls much of it is absorbed at once, without heavy run-off, and this water is later given up gradually to the creeks. In consequence of this, the streams are largely perennial and hence suited to the continuance of a stream-inhabiting amphibian such as the present species. *Boylii*, where it lives in the humid coast Transition Zone, is assured of sufficient moisture and, at the same time, of a stream current not dangerous to its eggs or larvae. The streams in the Transition Zone of the Sierra Nevada are different in character. Their courses are boulder strewn and precipitous, but these features in themselves are not necessarily of a character to deter a stream-inhabiting frog. The Sierran streams become swollen in early summer with the melting of the snows at the higher levels, and the rate of flow of the water in that season is so swift that amphibian larvae without special adaptive structures for holding their position in the stream would quickly be swept downstream and killed. It is this feature rather than the low temperature of the water which is the

limiting factor with *boylii*. That the cold mountain stream type of habitat is not closed to the use of an amphibian that is specially suited for life in such an environment is indicated in the life-history of *Ascaphus truei* (see Gaige, 1920). *Boylii* is found in the slower moving waters in the Upper Sonoran Zone, it is absent from the torrential streams in the Transition and Canadian zones, and it reappears again, in modified form (subspecies *sierrae*), at the higher altitudes in the slower streams and in the lakes of the Hudsonian Zone.

Rana boylii muscosa Camp. Sierra Madre Yellow-legged Frog

(Pl. 2, fig. 4; pl. 12, fig. 36)

Rana pretiosa, Yarrow and Henshaw (1878, p. 210), part. Locality record.
Rana pretiosa, Yarrow (1883, pp. 25, 186), part. Locality records.
Rana boylii muscosa Camp (1917*b*, pp. 118–120). Original description, type from Arroyo Seco Cañon, altitude about 1300 feet, near Pasadena, California.
Rana boylii muscosa, Grinnell and Camp (1917, pp. 147–148, fig. 5). Range.
Rana boylii muscosa, Stejneger and Barbour (1917, p. 36; 1923, p. 34). General range.

Diagnosis.—As for *Rana boylii boylii* (which see), but without light patch across upper eyelids in front of dark patches (except in young); dorsal ground color usually lighter, and tips of toes more expanded.

Comparisons.—See *Rana boylii boylii*.

MEASUREMENTS OF ADULT SPECIMENS OF *Rana boylii muscosa* FROM SAN GABRIEL MOUNTAINS, LOS ANGELES COUNTY, CALIFORNIA

M.V.Z. No.	Sex	Locality	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
4856	♀	Mt. Wilson trail below Half Way House	July 22, 1913	54 0	16 8	20.0	6 8	3.5	12.0	13.7	26 0	29.5	13.3	42
4388	♀	Little Santa Anita Cañon, 2800 ft.	June 23, 1909	57.0	18.7	21.0	7.0	4.0	13.2	14.5	28.0	30.6	14.2	45
4383	♀	West Fork San Gabriel River, 3000 ft.	May 1, 1909	62.5	19.7	24.0	7.8	4.6	16.0	16.0	35.0	34.0	16.8	51
6905	♀	Santa Anita Cañon at The Falls	May 5, 1918	66.5	20.5	25.0	8.0	5.0	17.0	17.5	39.0	37.5	18.0	54
4381	♀	West Fork San Gabriel River, 3000 ft.	May 1, 1909	67 6	21.5	26.0	8.2	4.0	16.8	16.4	36.0	37.0	18.3	56
4855	♂	Mt. Wilson trail below Half Way House	July 22, 1913	48.0	16 0	17 8	7.0	4.0	12.4	12.7	23.6	26.7	13.0	40
4387	♂	West Fork San Gabriel River, 3000 ft.	May 1, 1909	50 2	15.5	18.0	7.4	4.0	13.0	12.7	27.5	29.0	14.0	42
4374	♂	Little Santa Anita Cañon.	Apr. 5, 1908	55.5	18.5	19.8	6.1	5.0	15.0	15.0	29.2	31.2	14.0	47
6915	♂	In cañon, 1½ mi. n. Sierra Madre	May 30, 1918	55.8	18.5	20 6	8.8	4.0	15.2	14.0	29.5	32.0	14.2	48
770	♂	Arroyo Seco near Pasadena	Aug. 3, 1903	56 3	18 6	21.0	7.6	4.7	14.0	13.0	30.6	30.8	15.4	45

Range.—This form inhabits stream cañons in southern California, south of Tehachapi Pass. Localities of record extend from Pacoima Cañon near San Fernando eastward and southward along the southern and western slopes of the San Gabriel, San Bernardino and San Jacinto ranges as far as Keen's Camp, in the latter range. It has been found also at Little Rock Creek on the north slope of the San Gabriel Mountains. The range in altitude is from 1200 feet near Sierra Madre to 6500 feet on Fish Creek in the San Bernardino range (Camp, 1917*b*, p. 119; Mus. Vert. Zool.).

Life-history.—In most respects the habits of this species are like those of *Rana boylii boylii.* A mated pair seen in Santa Anita Cañon, near Monrovia, April 11, 1910 (Camp, MS) suggests breeding at about the same time as with the northern subspecies.

Rana boylii sierrae Camp. Sierra Nevada Yellow-legged Frog
(Pl. 17, fig. 51)

Rana pretiosa, Stejneger (1893, p. 226), part. Locality records in southern Sierra Nevada.

Rana boylii sierrae Camp (1917*b*, pp. 120–123, fig. 2). Original description, type from Matlack Lake, altitude 10,500 feet, 2 miles south of Kearsarge Pass, Inyo County, California.

Rana boylii sierrae, Grinnell and Camp (1917, p. 146, fig. 5). Range.

Rana boylii sierrae, Stejneger and Barbour (1917, p. 36; 1923, p. 34). General range.

Rana boylii, Boulenger (1920, pp. 469–471), part. Critical; range.

Rana boylii sierrae, Grinnell and Storer (1924, pp. 663–665, pl. 60*b*). General account; habits.

Diagnosis.—As for *Rana boylii boylii* (which see), but hind leg relatively shorter (posterior side of flexed tarsus reaching anterior border of orbit), toes more pointed, head relatively narrower, tympanic membrane smoother and light patch lacking on eyelid; dorsolateral folds indicated.

Comparisons.—See *Rana boylii boylii.*

Coloration.—Camp (1917*b*, pp. 121–122) says:

Three specimens from the southern Sierra Nevada and two from Young Lake, Tuolumne County, show faint traces of a lighter patch across the anterior part of the head, as in *R. b. boylii.* Nearly all the frogs from Whitney Meadows have the dorso-lateral folds unusually well developed. The dorsal color pattern varies widely. Occasionally the back is uniformly reddish-, brownish-, or blackish-yellow; more rarely it is evenly marbled with dark brown upon a dark yellow background with or without indefinite lighter spots; more frequently the darker markings remain as indefinite patches or as distinct black spots, thus approaching the pattern of *R. pretiosa.* The outline of the head viewed from above is either rounded as in the type or pointed as in *boylii;* in some specimens it is as wide as in the narrowest *boylii.*

This seems to be the subspecies of *boylii* which approaches most closely to the species *pretiosa.* A few specimens can be found in which the vomerine teeth are confined to the ends of slight swellings on the vomerine ridges, much as in *pretiosa* . . .; the outline of the head is in some specimens the same as in *pretiosa,* and the short hind leg carries the resemblance still farther. The dorsal color pattern, while usually quite different from that in *pretiosa,* suggests the latter in an occasional individual. I am inclined to place *sierrae* with *boylii* on account of the character of the vomerine teeth in most of the specimens . . ., the usual absence of distinct dorso-lateral folds, the mottling of the upper lip, the lack of red in the coloration of the under parts, and the suggestion of a white, anterior head-patch in seven or eight out of the 150 specimens examined.

MEASUREMENTS OF ADULT SPECIMENS OF *Rana boylii sierrae* FROM YOSEMITE NATIONAL PARK, CALIFORNIA

M.V.Z. No.	Sex	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
5970 [1]	♀	56.7	17.3	19.0	6.1	4.1	11.8	14.6	31.0	29.0	14.0	41
6013 [1]	♀	57.0	17.6	18.8	6.7	4.3	12.0	13.3	27.0	28.0	14.0	41
5979 [1]	♀	58.0	17.0	19.5	6.0	4.4	11.4	13.5	25.0	27.5	13.0	40
5987 [2]	♀	65.5	22.0	25.0	8.3	6.1	16.4	17.5	34.0	39.2	18.7	55
5996 [1]	♀	67.4	21.0	22.5	6.7	5.1	14.0	16.8	31.0	34.0	16.0	48
5998 [1]	♂	50.0	15.0	15.6	5.4	4.0	11.7	11.0	22.8	24.0	12.0	36
5999 [1]	♂	52.0	16.0	18.0	6.4	3.5	12.0	10.8	25.0	26.4	12.5	39
5963 [1]	♂	54.0	16.4	18.0	5.6	3.3	12.0	12.0	24.4	25.5	12.0	38
6019 [3]	♂	54.0	17.5	17.3	7.3	4.0	12.0	12.5	21.3	25.0	....	39
5991 [1]	♂	59.0	18.0	18.6	6.4	4.4	12.8	13.0	26.0	28.0	13.7	41

[1] Vogelsang Lake, 10,350 ft., Aug. 30, 1915.
[2] Sunrise Trail at 7300 ft., Aug. 19, 1915.
[3] Evelyn Lake, 10,350 ft., Sept. 6, 1915.

Range.—This frog is restricted to the alpine portions of the central and southern Sierra Nevada in California. It has been recorded from Taylor Meadow, 7000 feet, Tulare County, north to vicinity of Young Lake, Tuolumne County, in Yosemite National Park. The lowest station of record is that given above; this form occurs on Whitney Creek, Tulare County, at 11,500 feet, and in the head of Lyell Cañon, Yosemite National Park, at 10,500 feet. These two stations are both at, or very close to, timber line. In addition to the intermediate localities given by Camp (1917*b*, p. 121) this subspecies has been found at Huntington Lake, 7000 feet, Fresno County, and at Mammoth Lakes, 9200 feet, and Pine City, 8700 feet, Mono County (Mus. Vert. Zool.).

The status of the frogs of this group at Lake Tahoe is unknown.

Life-history.—The known facts concerning the life of this frog indicate that it differs considerably from the lowland races of *boylii*. Streams are inhabited by *sierrae* where available, but many individuals live in glacial lakes. Their habits in these places are, however, more like those of *boylii* than of the strictly pond-inhabiting frogs (*aurora* ssp.) elsewhere in California, as *sierrae* sits on rocks adjoining the lakes "within one jump of the water." A person's

. . . progress along the bank of a pool is announced by a series of splashes ten to twenty-five feet ahead, as the numerous frogs in quick succession take to the safety of the water. Once under the surface a few quick strokes of the hind legs with their broad foot-webs put the frog under some sheltering rock. The mottled pattern of the upper surface is quite protective in character when the animal comes to rest. When once on the bottom the frog is likely to remain there quietly unless further disturbed. When the frog is in motion, either jumping or swimming, the yellow color on the legs shows contrastingly against the dark upper surface of the body, but it is almost entirely masked when the frog is at rest (Grinnell and Storer, 1924, p. 664).

It seems likely that these alpine frogs winter in the lakes which form their summer habitat, going down deep enough to escape freezing.

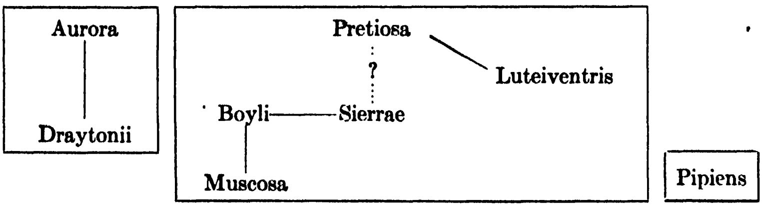
The spawning season of this subspecies is delayed until midsummer. On June 22, 1915, adults collected at Peregoy and Mono meadows, in Yosemite National Park, had, for the most part, deposited their eggs; some of the females collected at, and near, Tuolumne Meadows the same year during the first half of July had already laid, while others contained eggs ready to lay.

Eggs obtained in Cathedral Pass, Sunrise Trail, Yosemite National Park, on July 4, 1922, by Professor Stanley B. Freeborn, prove to be approximately like those of *boylii* in the lowlands. Exact measurements are not feasible, as the material was not fixed in a manner favorable to preservation of the original size.

In the foothill district, where there is a long spell of warm weather, the tadpoles (subspecies *boylii*) are able to grow to the size necessary for transforming into frogs in a single season. But with the high mountain animals (subspecies *sierrae*) the case is different. The eggs are not laid until June or July, and there is then but a short season, scarcely three months in length, before cold weather sets in again. Consequently the tadpoles which hatch from the eggs in any one season go through the winter still in the tadpole condition and do not transform into frogs until the following summer. Thus the numbers of tadpoles, 2 inches or more in length, found in Young Lake on July 8 and 9, 1915, came from eggs which had been laid in 1914. On the dates mentioned, many of the tadpoles had the hind legs fully developed and in all probability would soon have completed their metamorphosis (Grinnell and Storer, *loc. cit.*).

Some of these larvae were collected, but the preservation was so poorly done that they were useless for study. A point of importance yet to be determined is the structure of the mouthparts, as it may be expected to afford information concerning the relationships of the *boylii* and *pretiosa* groups of frogs.

The relationships of *sierrae* are with the *boylii* group of frogs; yet, as pointed out by Camp, the representatives of the present subspecies at Whitney Meadows resemble *pretiosa* in several ways. The group relations of our western species of *Rana*, as now understood by the present writer, are indicated by the following diagram.



Rana pipiens Schreber. Leopard Frog

(Pl. 17, fig. 52; text fig. BB)

Rana pipiens Schreber (1782, pp. 185–191). Original description, type from New York State.

Rana pipiens, Richardson (1915, p. 433). Occurrence at Lake Tahoe.

Rana pipiens brachycephala, Camp (1916*a*, p. 509). Along Colorado River Valley in California.

Rana pipiens, Bryant (1917, p. 92). Introduction at Lake Tahoe.

Rana pipiens, Grinnell and Camp (1917, p. 149, fig. 5). Range in California.

Rana pipiens, Stejneger and Barbour (1917, p. 38; 1923, p. 36). General range.

Rana halecina, Boulenger (1920, pp. 433–443). General account.

Diagnosis.—Size moderate among California frogs, head-and-body length up to 74 millimeters (2⅞ inches); head and body slender; tympanic membrane conspicuous, smooth-surfaced, with light spot at center; dorsolateral folds well developed, dorsal surface with sharply outlined dark spots, each outlined with lighter color; vomerine teeth in two compact clusters between internal nares.

Comparisons.—Distinguished from *Scaphiopus* by rounded pupil, slender form of body, and absence of cutting spade on hind foot; from Bufonidae by slender form of head and body and absence of parotoid glands; from Hylidae by larger size and absence of expanded discs on digits; from *Rana boylii* ssp. by slender head and body, conspicuous and smooth tympanic membrane, well-developed dorsolateral

folds, conspicuous black spots on dorsal surface, and compact grouping of vomerine teeth; from *Rana pretiosa* ssp. and *Rana aurora* ssp., by absence of light line on upper lip, by more conspicuous and smoother tympanic membrane, by absence of black patch on side of head, and by absence of red in coloration of ventral surface; from *Rana catesbeiana* by more slender form, presence of conspicuous dorsolateral folds, tympanic membrane smaller than orbit, and presence of black spots on upper surface.

Description (based on two adults from Imperial Valley and Colorado River).—Body slender, legs large; head very acutely oval in outline from above, pointed at tip, thin in profile, tip of muzzle slantingly rounded; external nares opening dorsally, about equidistant from tip of snout and anterior border of orbit on distinct canthus rostralis; side of muzzle below canthus rostralis slanted outward to margin of upper jaw; orbit large; interorbital space very narrow, not one-half length of orbit; tympanic membrane large, rounded, with distinct spot in center, diameter half (female) or two-thirds (male) of length of orbit; anterior border of tympanic membrane close to posterior margin of jaw; lower jaw narrowly oval, overhung at tip by upper jaw; fore limb moderate; exposed portion of upper arm shorter than forearm; palm short; two palmar tubercles, not conspicuous; sesamoid tubercles round; digits slender, pointed, third longest, first, second, and fourth subequal; body slender; dorsolateral folds conspicuous; hind limb very stout, tibia shorter than femur; tarsus rounded, about one-third of length of whole foot; foot slender; one inner elongate metatarsal tubercle; sesamoid tubercles oval; toes slender, tips not blunt, in order of decreasing length, 4, 3, 5, 2, 1; web reaching to middle of penultimate phalanx of fourth toe.

Tongue narrowly or broadly heart-shaped, pointed anteriorly, bilobed posteriorly, greatest width half (male) or two-thirds (female) width of mouth at angles of jaws, thicker in male than in female; maxillary teeth small, numerous, extending to angles of mouth; internal nares large, widely spaced, close to margin of jaw; vomerine teeth in two separate oval groups, between internal nares, convergent posteriorly.

MEASUREMENTS OF ADULT SPECIMENS OF *Rana pipiens* FROM CALIFORNIA

M.V.Z. No.	Sex	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
1845 [1]	♀	65.5	24.4	22.2	9.0	3.0	15.2	17.0	31.2	34.3	18.2	52
1058 [2]	♂	74.0	26.1	25.7	9.0	3.2	19.0	18.6	36.0	38.7	20.1	60
6196 [3]	♂	64.0	21.8	20.4	7.8	2.3	16.4	16.9	33.0	35.4	19.5	57

[1] Colorado River near Riverside Mtn., Mar. 21, 1910.
[2] 6 mi. w. Imperial, Imperial Co., May 6, 1909.
[3] Lake Tahoe (Placer Co.?), Sept., 1916.

Surfaces generally smooth; sides of body with low papillae; posterior surface of femur rugose; palms and soles smooth.

Color (in alcohol) dorsally, between lateral folds, dark brown, with scattered, irregularly rounded spots (up to 4 mm. in diameter) of black, faintly rimmed with white; dorsolateral folds pale gray or white; sides of body paler than back, blending ventrally into plain yellow or white of undersurface; sides variously spotted with black; exposed surfaces of limbs like back, with irregular spots (fore limb) or crossbars (hind limb) of blackish; tympanic membrane dusky yellow with whitish spot at center.

History.—Cope (1889) designated the western stock of this species as *Rana virescens* [= *pipiens*] *brachycephala*, designating Yellowstone River [in Montana?] as the type locality, but the name has not found general acceptance. The few specimens at hand from the lower Colorado basin and the neighborhood of Lake Tahoe differ in that the latter have the spotting characteristic of the species in the eastern states, whereas the animals from southeastern California have fewer and smaller spots and the white margining of the spots is less conspicuous.

Range.—This is the most widely distributed species of Salientian in North America. It is found from the Valley of Mexico northward to southern Canada (Quebec), and from the Atlantic coast west practically to the Sierra-Cascade divide (Cope, 1889, pp. 397–406). The western boundary of its range in California may be described more particularly as follows: Two miles east of Dixieland, Imperial County (Storer, MS), Riverside Mountain, Riverside County (Grinnell and Camp, 1917, p. 149), Fallen Leaf Lake, Eldorado County (Calif. Acad. Sci.), Lake Tahoe (Richardson, 1915, p. 433), and Alturas, Modoc County (Calif. Acad. Sci.). The species seems not to have been found in eastern Oregon. In Idaho it is known from Boise, Ada County (Van Denburgh and Slevin, 1921*b*, p. 42), and Sand Point, Kootenai County (Van Denburgh *in* Gilbert and Evermann, 1895, p. 207).

The status of *pipiens* at Lake Tahoe (Bryant, 1917, p. 92) is believed to be that of an introduced species; possibly the same is true at Alturas. An attempted introduction of *pipiens* in the northern Sacramento Valley was made in 1918 when stocks (source unknown) were planted on ranches east of Red Bluff (Elliot and Hickman ranches) and at Battle Creek Meadows [= Mineral Postoffice], altitude 4500 feet. Mr. D. G. Maclise, who was instrumental in placing these frogs, reported that in 1920 the frogs near Red Bluff were

"thriving"; but efforts to obtain specimens in 1924 were unavailing. *Pipiens* is the species of frog used most commonly in physiological laboratories, and is also sought commercially for 'frogs-legs'; other attempts of planting may therefore have been made within California.

Life-history.—The habits and life-cycle of this species have been described in detail by Dickerson (1906) and Wright (1914). In all probability the life-history of the *pipiens* stock at Alturas and Lake Tahoe resembles, in some degree, that of the species in the eastern states. In the Colorado Valley, and in the Imperial Valley (where this species has probably been carried as a result of the development of irrigation), suitable conditions for a marsh-inhabiting frog such as *pipiens* are to be found only along waterways.

Ruthven (1907, pp. 510–511) states that at Tucson, Arizona, this species is to be found only "about the margins of pools and irrigating ditches in the valley of the Santa Cruz River, and along the stream in Sabino Cañon. It is quite common in these habitats, but is closely confined to the vicinity of the water, a fact which limits the migration routes of the species in this region to the water courses." In a footnote this author says that "in the timbered and prairie regions of eastern United States this frog is often found a mile or more from water, having traveled this distance through damp underbrush or long grass. Its migration routes in this region are not, therefore, confined to particular streams."

Upon a visit to Imperial Valley on March 27 and 28, 1923, the present writer found *Rana pipiens* in some numbers in overflow ponds between Brawley and El Centro and in roadside ditches west of the latter town between Seeley and Dixieland. In a pool formed at the side of the main highway 2 miles east of Dixieland, a mass of eggs of this frog was found on March 28, 1923, and there were also ranid tadpoles of small size evidently from eggs deposited earlier the same month. This particular egg mass was attached to weed stems in the water, and was about 75 millimeters (3 inches) in diameter, though it was irregular in contour. It was larger than that of *Rana b. boylii* but smaller than that of *Rana a. draytonii.* Close study showed *three* distinct jelly coats, whereas Wright (1914, p. 17, fig. 1G) figures only two coats in material of *pipiens* collected at Ithaca, New York. The embryos in the Imperial Valley material had already begun to elongate, so that the size is probably slightly greater than in fresh material. Dimensions, in millimeters, were as follows:

	Egg	Vitelline capsule	Inner jelly coat	Middle jelly coat	Outer jelly coat
Minimum	1.67	1.78	2.00	2.22	4.23
Maximum	2.00	2.11	2.50	2.72	4.78
Average of 10	1.80	1.97	2.25	2.35	4.48

Rana pretiosa pretiosa Baird and Girard. Western Spotted Frog

Rana pretiosa Baird and Girard (1853*b*, p. 378). Original description, type from Puget Sound.

Rana temporaria pretiosa, Cope (1889, pp. 432–434, text fig. 110), part. General account.

Rana pretiosa, Chamberlain (1897, pp. 255, 258; 1898, p. 259). Economic status.

Rana pretiosa, Dickerson (1906, pp. 218–221, col. pl. 16, pl. 83 [figs. 260–263]). General account; breeding habits.

Rana pretiosa pretiosa, Camp (1917*b*, pp. 123–124). Characters; general range.

Rana pretiosa pretiosa, Grinnell and Camp (1917, p. 148, fig. 5). Range in California.

Rana pretiosa pretiosa, Stejneger and Barbour (1917, p. 38; 1923, p. 36). General range.

Rana pretiosa, Boulenger (1920, pp. 452–455). General account.

Diagnosis.—Size moderate among California frogs, total length up to 73 millimeters (2⅞ inches); hind leg proportionately short, inside angle of flexed tarsus not reaching beyond external naris; vomerine teeth grouped in two clusters between internal nares; fold of skin along upper lip light colored; back with numerous inky black spots; two metatarsal tubercles; ventral surface of body and hind limbs often red.

Comparisons.—Distinguished from *Scaphiopus* by absence of cutting spade on hind foot; from Bufonidae by absence of parotoid glands and presence of teeth, from Hylidae by absence of expanded discs on digits; from *Rana boylii* ssp. by concentration of vomerine teeth between internal nares, larger size of maxillary teeth, presence of white fold of skin along upper lip, presence of inky black spots on dorsal surface, and presence of red in ventral coloration; from *Rana aurora* ssp. by shorter hind leg (inside angle of flexed tarsus not reaching beyond external naris), and presence of black spots not margined with lighter color on back; from *Rana pipiens* by less acute outline of head, smaller tympanic membrane, less well-developed dorsolateral folds, absence of white margins around dark spots on back, and presence of red in coloration; from *Rana pretiosa luteiventris* by presence of two metatarsal tubercles, by presence (usually) of two palmar tubercles, by greater number of, and larger, blacker spots on dorsal surface, and by deeper tone of red in coloration of ventral surface.

Description.—Form moderate, body slender, legs long; head acutely oval in outline from above, muzzle thin, slanting in profile; external nares below beginning of distinct canthus rostralis, nearer tip of muzzle than orbit, opening dorsally; side of muzzle below canthus rostralis slightly concave; orbit moderate; interorbital space flat, half to four-fifths length of orbit; tympanic membrane round, close behind and below orbit, its greatest diameter about two-thirds length of orbit; conspicuous raised and rounded ridge originating below anterior margin of orbit, extending posteroventrally to near origin of fore limb; short diagonal fold of skin from posterior margin of orbit extending obliquely over tympanic membrane to above fore limb; outline of lower jaw truncate-oval; fore limb slender; exposed portion of upper arm about equaling forearm in length; hand long, exceeding forearm in length; palm with one or two elongate low tubercles; sesamoid tubercles large and conspicuous; digits slender, in order of decreasing length, 3, 4, 2, 1, the latter three subequal; body ovate in outline from above; dorsolateral folds distinct, originating at diagonal ridge behind orbit; hind limb moderate; tibia equaling or exceeding femur; tarsus about one-third length of foot; length of foot about five-sixths length of head-and-body; metatarsal tubercles two, outer (opposite fourth toe) decidedly smaller than inner; subarticular tubercles round, smaller than on hand; toes long and slender, in order of decreasing length, 4, 3, 5, 2, 1; web large and thin, shallowly scalloped.

Tongue thick, broadly heart-shaped, bluntly pointed in front, bilobed behind, about half width of mouth at angles of jaws, attached by anterior two-thirds to floor of mouth; internal nares oval, close to sides of mouth; maxillary teeth numerous but rather small; vomerine teeth at inner ends of two oblique ridges between and slightly behind internal nares.

Surfaces generally rather smooth; dorsal surface of body evenly and finely roughened in old individuals; palms and soles smooth, save for tubercles described above; ventroposterior surfaces of thighs with close-set rounded papillae.

Color (in alcohol) above, yellowish brown of light or dark shade, beset with few or many various-sized irregular spots of inky black (not margined with lighter color); limbs crossed by obscure bars of blackish; ridge along upper lip white; under surface clear yellow sometimes mottled with blackish on chin, throat, and sides of body; under surfaces of hands and feet, dusky.

Live specimens from Seattle, Washington, presented the following coloration in life: dull or bright yellowish or reddish brown on head, back, and upper surfaces of arms and legs; back between dorsolateral folds with few or many irregular roundish spots (like splashes of ink) of black; lower sides light yellowish gray, unspotted; under surface light, marbled obscurely or conspicuously with grayish brown; under surface of legs and sides and posterior part of belly salmon red; streak along upper jaw, light; iris bright yellow, not orange-colored or bronze (adapted from Dickerson, 1906, p. 218).

MEASUREMENTS OF ADULT SPECIMENS OF *Rana pretiosa pretiosa* FROM NORTHEASTERN CALIFORNIA

M. V. Z. No.	Sex	Date	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
9093[1]	♀	Sept. 12, 1923	59.0	19.1	20.5	6.5	3.3	14.5	14.9	30.7	31.7	16.4	44
9087[1]	♀	Sept. 8, 1923	60.5	18.7	21.2	6.3	4.0	15.5	16.8	31.6	31.4	17.0	49
9096[1]	♀	Sept. 13, 1923	62.5	20.2	21.6	6.9	3.7	15.0	16.3	33.2	32.2	17.3	46
9095[1]	♀	Sept. 13, 1923	63.2	19.3	21.7	6.3	4.1	15.0	15.3	32.2	31.7	17.0	44
5568[3]	♀	Aug. 10, 1914	73.6	23.2	24.3	8.7	3.7	17.6	17.8	35.5	40.0	21.0	56
9094[1]	♂?	Sept. 12, 1923	43.0	14.8	16.0	4.4	2.3	12.0	12.0	22.7	23.6	12.3	37
9083[4]	♂?	Sept. 6, 1923	45.0	15.5	16.4	5.5	3.0	12.0	12.0	23.5	26.3	13.0	38
9101[2]	♂	Sept. 28, 1923	45.0	15.5	17.0	5.4	3.0	11.8	12.8	23.2	23.6	13.0	38
5566[3]	♂?	Aug. 9, 1914	64 1	21.3	24.0	8.5	5.6	15.6	....	36.5	37.8	20.5	56

[1] Warner Creek, 8000 ft., Lassen Peak.
[2] Warner Creek, 6600 ft., Lassen Peak.
[3] Sisson, Siskiyou Co.
[4] Hot Springs Valley, Plumas Co.

Range.—*Rana pretiosa pretiosa* has been found at the south in California at Hot Springs Valley and on Warner Creek at 6600 and 8000 feet on the slopes of Mount Lassen in Shasta County (Mus. Vert. Zool.). A specimen taken at "Summit Johnson's Pass, Sierra Nevada" in September, 1863, by J. G. Cooper (now no. 8263, Mus. Vert. Zool.) is probably to be referred to this species. *Pretiosa* has also been found at Sisson (Grinnell and Camp, 1917, p. 148). I can find no record for *pretiosa* in Oregon west of the Cascades. Nothing is known of the frog population of that range. The *pretiosa* stock in eastern Oregon probably all pertains to subspecies *luteiventris*. In Washington, *pretiosa* has been found at Crescent Lake, Clallam County (Meek, 1899, pp. 232–233), at Seattle (Dickerson, 1906, p. 219), on Mount Rainier (Van Denburgh, 1912*c*, p. 259; Calif. Acad. Sci.), and at Springdale, Stevens County (Blanchard, 1921, p. 6). In British Columbia, *pretiosa* has been recorded at Sumas Prairie (Boulenger, 1882*a*, pp. 43–44), at Sicamous and Field (Cope, 1893, p. 182), and at Watson Lake, Meadow Lake, and Clinton (Patch, 1922, p. 78). The Museum of Vertebrate Zoology has specimens taken in British Columbia on the Skeena River at Hazelton and in the Kispiox Valley adjacent, during the summer of 1921, and on the Stikine River near Telegraph Creek, at Flood Glacier, and at Doch-da-on Creek, obtained during 1919. At the mouth of the latter river, in southeastern Alaska, *pretiosa* was found in 1919 on Sergief Island. This

is, to the best of my knowledge, the first evidence of the occurrence of this frog in the northwestern part of British Columbia and also of its presence anywhere in Alaska. "*Rana pretiosa*" has been recorded at numerous localities in the interior, but the subspecific status of these records has not been ascertained since Gaige in 1913 described *Rana pretiosa luteiventris*. On geographical reasoning some of these records might be expected to belong to the latter subspecies. The records are given here merely as pertaining to *Rana pretiosa* in order to outline the range of the species as fully as possible.

Cope (1879, p. 435) records a specimen from Prickly Pear Cañon near Fort Benton, Montana. Cary (1917, p. 33) lists *Rana pretiosus* [=*pretiosa*] from Wyoming, stating that it is more abundant in the Transition than in the Upper Sonoran Zone. Van Denburgh and Slevin (1921*b*, p. 42) record it in Idaho from Payette Lake and McCall, Boise County, and Guyer Hot Springs, Blaine County; the same authors (1915, p. 102) record one specimen from Fort Douglas, Utah, and a large number from Provo Cañon, Wasatch Mountains, Wasatch County. These authors evidently reject *luteiventris*, as they state that they are unable to find constant differences in coloration or in plantar or palmar tubercles between these Utah specimens and others from Fort Klamath, Oregon, and Mount Rainier, Washington.

Life-history.—*Rana p. pretiosa* in California occurs in pools or marshes along perennial streams and in springs. It is a highly aquatic species. While specifically distinct from the *aurora* group it resembles the latter in habits. The ecologic requirements of the two are much alike, and present information suggests that the two are almost, if not entirely, complementary in distribution. They occur together in the moist part of western Washington, where presumably the aquatic environment is more diversified than in other parts of the West (see p. 18).

Dickerson (1906, pp. 218–219) on the basis of data furnished by Professor J. F. Illingsworth gives the following information concerning the life-history.

> The Western Frog has been found during the winter, sleeping in the mud under a foot or more of water, along marshy lake margins. It appears in the Puget Sound region from the last of February to the middle of March. A few scattered individuals may, however, be seen on sunny days throughout the winter. These are usually among the lily-pads along the marshy borders of the lakes.
>
> As soon as they appear in March, they set up a noisy croaking, and the eggs are laid between this time and the first of April. The egg-masses . . . are un-

attached. They vary greatly in size, but average about a pint in bulk. In one case where the eggs were counted, a laying consisted of over fifteen hundred eggs. The eggs are relatively large, measuring nearly 2 mm. in diameter. Each egg is in a transparent sphere of jelly measuring one-half inch across. The eggs are placed in the shallow, marshy pools near a lake, but never in the deep lake-water itself. The length of time required for hatching is from one to two weeks, varying with the temperature; those in the warm, shallow water hatching earlier than those in deep water. The later development is slow, and it is not until after the summer is passed that the tadpole becomes a frog. This development is perhaps correlated to [with] the conditions of the region of the frog's range. There is an abundance of water in this region, even in summer, so that the development is not hastened by the drying up of the pools.

From this time on the growth is slow; at least, there can be found, each spring, frogs of four or five different sizes, so that it would seem as though they require four or five years to reach the adult size.

Blanchard (1921, p. 6) says that at Springdale, Stevens County, Washington, this species is common along streams but nowhere plentiful. "A stupid frog, easily caught; neither a strong jumper nor a fast swimmer. The salmon color of the underside is absent from the newly transformed adult; it increases in extent and brilliancy with increase in size, occasionally overspreading nearly the entire under surface of a large adult."

A young individual of *pretiosa*, 26.4 millimeters in head-and-body length, hence of the season's brood, collected on Warner Creek, altitude 6600 feet, Shasta County, California, September 19, 1923, is a partial albino, lacking entirely the black normally present in the coloration of this subspecies. The spots on the back are here brown; the dorso-lateral folds are pale yellow where normally dark brown, the limbs pale yellow, the location of the normal blackish crossbars being indicated by slightly darker yellow. The mottled pattern of the throat region, normally dusky, is indicated by faint yellow. This is the first instance of partial albinism which has come to attention in the present study of the amphibians of California.

Rana pretiosa luteiventris Thompson. Nevada Spotted Frog

Rana temporaria pretiosa, Cope (1883, p. 433). In Modoc County, California.

Rana pretiosa luteiventris Thompson (1913, pp. 53–56, pl. 3 [figs. 2, 3]). Original description, type from Anne Creek, Elko County, Nevada.

Rana pretiosa luteiventris, Camp (1917*b*, pp. 123, 124). Characters; occurrence in California.

Rana pretiosa luteiventris, Grinnell and Camp (1917, p. 148, fig. 5). Range in California.

Rana pretiosa luteiventris, Stejneger and Barbour (1917, p. 39; 1923, p. 36). Range.

Diagnosis.—As for *Rana pretiosa pretiosa* (which see), but palmar tubercles reduced or absent, outer metatarsal tubercle absent, coloration of back paler, with fewer black spots, and coloration of under surface more orange.

Comparisons.—See *Rana pretiosa pretiosa.*

Description of larva.—Length of body 34 mm.; width 22 mm.; length of tail 67 mm.; height 13 mm.; external nares nearer orbits than tip of snout; internarial distance half of interorbital space; legs well developed, small but distinct tubercle at base of fourth toe; spiraculum sinistral; anal opening dextral, in ventral part of caudal fin; labial teeth in $\frac{2}{3}$ rows, second row broadly interrupted medially, fifth row short, about as wide as lower horny jaw; "color in alcohol brownish grey above, with lateral folds a little lighter; belly greyish white; muscular part of tail yellowish white with small grey spots; caudal crests grey with darker spots." [From Thompson, 1913, p. 54: specimen older than those used in other larval descriptions in present paper.—T. I. S.]

MEASUREMENTS OF ADULT SPECIMENS OF *Rana pretiosa luteiventris* FROM CALIFORNIA AND OREGON

M.V.Z. No.	Sex	Head-and-body body	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
7491[1]	♀	55.4	17.2	18.6	6.3	3.5	11.8	13.8	27.3	28.2	16.5	45.5
7490[1]	♀	63.4	19.6	20.7	6.4	3.5	14.4	15.0	31.6	30.6	17.8	46.5
7493[1]	♀	63.5	18.4	20.1	6.6	4.2	14.7	16.8	30.0	32.4	18.4	50
2098[2]	♂	53.2	16.0	15.3	5.8	3.8	....	....	22.5	23.9	10.2	38
7492[1]	♂	55.6	16.9	18.2	6.3	3.5	13.0	13.7	26.8	27	16	46

[1] 10 mi. w. Prineville, Crook Co., Ore., July 25, 1920.
[2] S. fork Pit River near Alturas, 4600 ft., Modoc Co., Calif., June 9, 1910.

Range.—This interior form of the *pretiosa* group was described from northeastern Nevada. Specimens referable to this subspecies are at hand from Prineville, Crook County, Oregon, and Butte Creek, Siskiyou County, California (Mus. Vert. Zool.) [the latter intermediate toward *Rana p. pretiosa*]. It has already been recorded from Pine Creek, near Alturas, Modoc County (Camp, 1917*b*, p. 124; Grinnell and Camp, 1917, p. 148). Cope (1889, p. 433) says that he obtained *Rana temporaria pretiosa* [= *luteiventris*] "the entire length of the valley of the Warner Lakes, but not at Fort Bidwell." Specimens from Pendleton, Umatilla County (Van Denburgh *in* Gilbert and Evermann, 1895, p. 207), and Island City, Union County, Oregon (Van Denburgh, 1912*a*, p. 159) probably belong here, as also speci-

mens listed from Fort Walla Walla, Washington (Cope, 1889, p. 434). Two specimens from Humpeg Falls, Columbia County, and Butte Creek, Blue Mountains, in eastern Washington (nos. 5586, 5587, Mus. Vert. Zool.), are referable to this subspecies. The line of separation between *luteiventris* and *pretiosa* remains to be determined.

Life-history.—*Thompson* (1913, pp. 54–55) says that in northeastern Nevada this frog was common in irrigation ditches.

It is quite aquatic, although the stomach contents, consisting of ants and water insects, indicate that at least part of the hunting is done on land. A few young specimens were taken a short distance from water on the banks of Anne Creek, but the adults were usually found along the edges of swiftly flowing streams or with only the head projecting from the vegetation of stagnant pools. When disturbed, they slipped quietly under the surface, but quickly reappeared, usually in the same place. Although they were almost as common as *Rana pipiens*, the two species were seldom found in the same pond.

The larva described above was collected on July 10, 1912, on which date, according to the description given by Thompson, the dorsolateral folds were in evidence and the hind legs were well developed; this would suggest a breeding season in March or April.

Introduced Species

Rana catesbeiana Shaw. Eastern Bullfrog

(Pl. 18, figs. 53–56; text fig. DD)

Rana catesbeiana Shaw (1802, pp. 106–108, pl. 33). Original description, type from (eastern) North America [=Carolina?: see Stejneger and Barbour, 1917, p. 37.]

Rana catesbeiana, Storer (1922, pp. 219–224, figs. 86, 87). Introduction and occurrence in California.

Diagnosis.—Largest Salientian in California; head-and-body length up to 175 millimeters (7 inches); skin of back relatively smooth, without dorsolateral folds; tympanic membrane equaling (females) or exceeding (males) diameter of orbit; a smooth, rounded ridge behind orbit and around dorsal and posterior margins of tympanic membrane; tympanic membrane of females concolor with body, of males dark brown marginally, with raised central portion of same color as body; no red anywhere on under surface of body.

Comparisons.—Distinguished from all other California Salientia by larger tympanic membrane; from other species of *Rana* by larger adult size, relatively smooth upper surface, and by absence of dorsolateral folds; from *Rana aurora* ssp. and *Rana pretiosa* ssp. by absence of red in coloration.

Description.—Size large, body stout, legs moderately heavy and toes of hind feet very fully webbed; head thin in profile, pointedly oval in outline from above; canthus rostralis slight; external nares opening just below canthus rostralis; eyes prominent; interorbital width about one-half length of orbit; side of head below eye smooth, grading insensibly into surface of tympanic membrane in female, separated by a slight ridge in male; a conspicuous smooth, rounded fold of skin (1 to 3 mm. wide) from hind border of orbit over dorsal and posterior margins of tympanic membrane to shoulder region; back relatively smooth, without dorsolateral folds; exposed portion of upper arm shorter than forearm; palm short, without obvious tubercles; digits long, in order of decreasing length, 3, 4, 1, 2; hind limb much heavier than fore limb; femur longer than tibia; one elongate inner metatarsal tubercle; sesamoid tubercles small; toes in order of decreasing length, 4, 3, 5, 2, 1; web large, not scalloped, including all toes except terminal phalanx of fourth toe.

Surfaces generally smooth in young individuals, somewhat roughened in old adults; under surface of body smooth; anal region slightly granular.

Tongue wedge-shaped, bilobed behind, rounded at front, width about half that of mouth at angles of jaws; maxillary teeth numerous, close set, around entire margin of jaw; internal nares very large, transversely oval; vomerine teeth in two concentrated clusters in broadly V-shaped arrangement, between internal nares.

General color of upper surface cress green, with numerous spots of dull bone brown (shading to blackish at centers of larger spots); upper jaw below naris and orbit, near Killarney green; iris mixed golden yellow and black; tympanum cress green, darker centrally, margin mixed brownish and dark cress green; ground color of foreleg cress green, tinged with brownish and spotted with blackish; ground color of hind leg varying from dull cress green on dorsal surface to grayish olive on tarsus; thigh with five or six crossbars and lower leg with four or five crossbars of dark brown or blackish; outer side of tarsus with three heavy blackish bars; toes spotted dorsally with blackish; chin wax yellow; belly whitish with faint suggestions of dark spots; buttocks mixed blackish and pale yellow in mottled pattern (based on live male from El Verano, Sonoma County).

Description of larva (based on second-year tadpoles from Sonoma Creek and Standard).—Total length 113 to 135 mm.; head-and-body 41–50 mm.; greatest width of body 22–30.3 mm.; internarial width 5.3–6 mm.; interorbital width 8–12.5 mm.; spiraculum sinistral, aperture directed backward and slightly upward, center of aperture about midway of body length; greatest height over tail fins 25 mm.; height of muscular part of tail 12–17 mm.; greatest width across mouth region 7.8 mm.

Coloration in life: Upper surface of body greenish olive to dark olive, with many minute specks of black; sides of tail with spots (up to 2 mm. in diameter) of yellow; under surface of body yellow to white, sometimes mottled with dusky, never iridescent; iris golden yellow. Labial teeth in $\frac{2}{3}$ (or $\frac{3}{3}$) rows, above mouth, uppermost complete, next divided, on either side of mouth, third row if present

including only a few teeth on either side; fourth row, below mouth, divided in midline, fifth complete across entire mouth region, sixth undivided but shorter than fifth; papillae at sides of mouth area in three rows, extending in part along lower border; one row of papillae bordering mouth region midventrally (fig. DD).

MEASUREMENTS OF SPECIMENS OF *Rana catesbeiana* FROM CALIFORNIA

M.V.Z. No.	Sex	Head-and-body length	Length of head	Width of head	Orbit	Interorbital space	Forearm	Hand	Femur	Tibia	Tarsus	Whole foot
8574[1]	♀	120.0	42.5	45.7	12.7	6.0	29.0	30.0	59.5	55.0	32.0	91
8575[1]	♀	125.0	44.5	45.6	11.7	6.0	31.0	33.0	65.0	58.0	34.0	96
8564[2]	♂	128.0	48.0	51.0	13.0	6.0	33.0	36.0	66.0	63.7	36.7	102
8576[1]	♂	129.0	48.0	51.5	14.0	8.0	32.0	30.0	70.0	61.0	34.5	93
8578[3]	......	49.5	17.3	17.6	6.5	3.2	10.9	11.3	26.4	24.0	13.3	39
8579[3]	......	48.3	16.8	17.3	6.7	2.8	9.5	12.5	23.0	24.6	13.6	39.5
8580[3]	......	45.0	16.0	14.5	6.4	....	8.6	10.8	21.5	19.8	11.0	34

[1] Mockingbird Lake, Riverside Co., July 23, 1922.
[2] El Verano, Sonoma Co., July 11, 1922.
[3] Agua Caliente, Sonoma Co.; nos. 8578–8580 collected as second year larvae, August 27, 1922, metamorphosed in captivity, and preserved on October 27, 1922.

Range.—Introduced into California. Adult specimens have been received at the Museum of Vertebrate Zoology from Sonoma Creek at El Verano and Agua Caliente, Sonoma County, and from Mockingbird Lake, near Riverside. Tadpoles have been received from Littlejohn's Creek at Farmington, San Joaquin County, and from a mill pond at Standard, Tuolumne County. The species is reported on good authority from Searsville Lake, Stanford University, Santa Clara County. It is said to be present in Little Lake, Inyo County. (See Storer, 1922, pp. 219–224.) Mr. E. P. Chace of Saugus has reported to the writer that he heard bullfrogs and saw large pollywogs at Resting Spring, Inyo County, in April, 1922. Mr. A. W. C. T. Herre, who formerly lived at Los Gatos, has told the writer that there were Eastern Bullfrogs in the creek in Los Gatos prior to 1910. The species has possibly been introduced in other localities in the State and a general increase in area occupied will probably be observed with the passage of the years.

In eastern North America, *Rana catesbeiana* occurs naturally from New Orleans and northern Florida northward to Montreal, and westward to Fort Smith, Arkansas (Cope, 1889, p. 427). The life-zones represented in the range there are Lower Austral (the eastern

analogue of Lower Sonoran in the west) to Canadian. In California the localities in which it has been planted are in the Lower and Upper Sonoran zones; two are just at the Upper Sonoran-Transition boundary.

The Bullfrog has been introduced into several places outside its own large range. Van Denburgh and Slevin (1921*b*, pp. 41–42) report that it was introduced into Idaho some years prior to 1916 and was then spreading rapidly. They record numerous specimens taken near Boise, Ada County. In the Hawaiian Islands several species of Asiatic and American frogs have been introduced, including *Rana catesbeiana* (Bryan, 1915, p. 297). The latter is now present in such numbers that it is sought commercially, and Hawaiian-grown Bullfrogs are to be found at times in the San Francisco markets.

The Bullfrogs introduced into California have come from at least three sources. Those in Sonoma Valley were obtained from a dealer in New Orleans and presumably came from Louisiana; those introduced at Farmington were obtained in Missouri, while the frogs at Standard are said to have been obtained from a San Francisco dealer who purchased his stock in Hawaii.

Three specimens of Bullfrog obtained at Mockingbird Lake near Riverside presented an appearance suggestive of that of *Rana grylio* Stejneger (1901, pp. 211–215), the Florida Bullfrog. Measurement of the Riverside specimens, however, shows that they are to be referred to *Rana catesbeiana*. Similarly, two frogs from the Sonoma Valley are *catesbeiana*.

Life-history.—Little is known as to the details of the Bullfrog's life-cycle in California. In the eastern states the species is almost exclusively a pond-dweller and practically never leaves the water. The same is apparently the case here. At Ithaca, according to Wright (1914, pp. 77–78), the Bullfrog is the last anuran to emerge from hibernation, appearing there only when the air temperature has reached 69° F. or higher, in May or June. It does not spawn until June or July. The early arrival of suitable air temperatures may induce an earlier appearance in California. At Searsville Lake, Stanford University, Mr. Richard Hunt (MS) heard Bullfrogs croaking on April 25, 1920. The frogs on Littlejohn's Creek and at Standard are reported not to emerge until April. The frogs reported at Resting Springs were heard during April; at Farmington, Bullfrogs were heard for a few days during January, 1923.

The voice of the Bullfrog is the loudest of any of the North American amphibians. The notes have been reported as being heard in most of the California localities into which the species has been introduced; indeed, people, living at Loma Linda, Riverside County, are said to have complained of the noise made by the frogs introduced near that place. No first-hand account of the voice of the Bullfrog is available from California, so a description given by Dickerson (1906, p. 232) may be quoted in part.

> The Bullfrog does not sing in chorus; the call is an isolated one. The notes are so low in pitch that we think of him as the bass viol among the batrachia. The call resembles, to a considerable degree, the roar of a distant bull but it has a more musical ring and the notes are less blended and slurred. The pitch varies with the individual. . . . The call can be imitated well by saying with a hoarse, deep-toned voice the syllables of various interpretations of it, such as, 'Be drowned,' 'Better go round,' 'Jug o' rum,' or 'More rum.' The imitation is especially good if the slurred words are repeated in front of some reverberating hollow body.

The Bullfrog has also, according to this and other authors, a loud prolonged high-pitched scream, uttered when the frog is seized by some large enemy.

No eggs laid in California have been available for study. The following description is condensed from an extended account by Wright (1914, p. 82), who studied this species at Ithaca, New York. The eggs are deposited in pond water of varying depth, usually around brushy material in the water. The egg mass is typically of disc form, loose in texture, and covers more than a square foot of area; exceptionally it may occupy as much as five square feet. Less often the eggs are deposited in stringy filaments. The complement may be from 10,000 to 20,000 eggs. The individual egg has a black animal pole and white or creamy white vegetative pole. The vitelline capsule usually measures 1.2 to 1.4 millimeters in diameter. There is no distinct middle envelope of jelly as with native California frogs, and the outer jelly coat, which is very loose, measures 6.4 to 10.4 millimeters in diameter.

The approximate time of egg deposition in California is indicated in one instance. On August 27, 1922, the writer found in Sonoma Creek opposite Agua Caliente a large mass of soft material which appeared very much like the remains of a Rana egg mass after the larvae had hatched out. Nearby in the creek were 'schools' of small ranid tadpoles measuring about 12 to 15 millimeters, a thousand or more in total number. These corresponded fairly well with the

description given by Wright (1914, pp. 82–83) for the first-season tadpole of *Rana catesbeiana,* save that they were smaller. A spawning date in midsummer is indicated in this case.

The Bullfrog in the eastern United States requires two full years (sometimes more) in order to complete its larval development. The situation in this respect in California is, inferentially, the same; direct observation is as yet to be made. According to Mr. Edmund C. Jaeger, high school students at Riverside stated that tadpoles in that neighborhood require two years to change into frogs. Further evidence of a lengthened larval life is furnished by material obtained by the writer in Sonoma Creek at Agua Caliente, Sonoma County, on August 27, 1922. On this date there were, in the pools of the creek, tadpoles of three distinct sizes. (The largest measured 135 millimeters in total length; and these all had fully developed hind legs and in many the forelegs had already burst through the opercular membrane.) The second category comprised tadpoles about 50 millimeters in total length, but without hind legs. Both of these lots of tadpoles were olive green in general coloration, with many fine black dots. The third lot was of very small tadpoles, about 12 to 15 millimeters in total length, of a generally black coloration with scattered yellow markings and an angular cross-mark on the back behind the eyes.

These three sizes of tadpoles correspond to the two-year-old, one-year-old, and newly hatched tadpoles of *Rana catesbeiana* as described by Wright. The inference seems justified that they represent egg masses laid in 1920, 1921, and 1922, respectively, and that the life-history of the Bullfrog in California is therefore essentially like that in the eastern states. So far as known, the only native California frog which regularly spends more than one season in the larval stage is *Rana boylii sierrae.*

The life-history in relation to the environment.—The introduction of the Bullfrog into California, while done in the first instance by laymen intent upon adding a desirable species to our rather meager frog fauna, is likely to provide, as an unintended by-product, material for an interesting study on the relation of the life-cycle of a species to its environment. The case is somewhat parallel to that afforded by the introduction of the English Sparrow, as recently discussed by Grinnell (1919). Fortunately the several localities into which the Bullfrog has been introduced are situated in several distinct biological regions of California: on the Mohave Desert, in the San Joaquin Valley, in the Sierran foothills, and in the Coast Ranges. As yet

practically no data are available concerning the seasonal programs of the populations in these various localities. It is to be hoped that such observations will soon be made and published in order that a basis will be provided to study the matter of possible changes in habits.

Here in California, as in the eastern states, *catesbeiana* is to be found only in places affording permanent pools of water. In fact, only in such situations can the species persist, because of the two-year period of larval life. It is likely that the stocks of adult frogs would perish in the absence of pools of water. In these respects the conditions in California resemble those in the native habitat of the species. But the temperature cycle in California is very different from that in the east. In the northeastern states the Bullfrogs hibernate during the several winter months when freezing temperatures prevail. In the California localities where this species has been planted (except at Standard) freezing temperatures are seldom encountered. The air and water temperatures which accompany the spawning of the Bullfrogs at Ithaca, New York, as ascertained by Wright (1914), are reached here much earlier in the season. If temperature *is* the governing factor, then the seasonal program of *catesbeiana* in California ought to be somewhat earlier than in the eastern states.

Inasmuch as one and perhaps other of the imported stocks of *catesbeiana* in California originated in New Orleans, it is important to know the time of spawning for the species in the southern states, but unfortunately there seem to be practically no data available. Strecker (1910), at Waco, Texas, gives the time of spawning as April 1 to May 10. Study of the effect in this respect of the environment on the Bullfrog in California must await publication of data for the species in the Gulf States.

SUMMARY

1. The present paper is a general synopsis of current knowledge concerning the amphibia of California, together with the results of studies by the writer on the life-histories of the eight common aquatic spawning species.

2. In the case of each species an effort is made to point out the factors in the environment which seem to be importantly correlated with the various stages in the life-cycle of that species.

3. Comparison of the life-cycles of California forms with those of analogous species inhabiting northeastern United States indicates that here moisture conditions are apparently the more important, whereas in the east temperature plays the leading rôle. This is not to be taken to mean that the western species are removed from control by temperature, but rather that the action of temperature in a critical way is largely suspended here by reason of the fact that the minimum and mean temperatures are, at all times, high enough to permit activity on the part of amphibians.

4. The breeding season for the common aquatic amphibians of central California is advanced into the months of January to April (see text fig. F), in, or immediately following, the period of maximum seasonal precipitation. Amphibians here would be permitted, so far as temperature is concerned, to spawn at practically any time of year. However, water ordinarily becomes available only at some time after the beginning of the rainy period, and it continues available, on the average, only for about two months after the end of that period. Breeding activity of the local species is concentrated into this period, save as the species, individually, have special adaptive adjustments to circumvent the generally dry conditions prevailing in the summer season.

5. Evasion of drought conditions is accomplished by several species by restricting their activities to small foothill streams (*Hyla arenicolor, Rana b. boylii, Rana b. muscosa*); others, the plethodont salamanders, carry on their spawning operations in damp situations at, below, or above the ground surface, without reference to water in pools or streams.

6. The important features discovered in the life-histories of the commoner California amphibia here studied are as follows:

a. Triturus torosus. Most terrestrial of all the aquatic spawning salamanders, with a definite dermal specialization to resist desiccation. It spawns early, the larvae are secretive, inhabiting pools in cañon bottoms, and metamorphosis occurs at about the time of the first autumn rains.

b. Ambystoma californiense. A close relative of the wide-ranging *Ambystoma tigrinum* inhabiting lowland areas in central California. The adults take shelter in various subterranean retreats to escape death by desiccation during the daytime. Spawning is advanced into the 'winter' season when the ephemeral rain pools are first formed and the larval period is relatively short, transformation occurring in late spring or early summer before the pools dry up.

c. Dicamptodon ensatus. This, the largest terrestrial salamander in North America, is confined to a relatively narrow strip of territory along the Pacific Coast where the ground is always moist and the atmosphere relatively high in moisture content. This species possesses a soft moist skin and can easily be killed by exposure to dry air. It spawns in large permanent pools on the courses of perennial streams and the larvae may continue in the water for more than one season before metamorphosis. Sexual maturity may be reached before metamorphosis. In the northwestern humid coast belt the aquatic habitat is permanent and an amphibian which remains there is assured the three essentials for existence, food, shelter from enemies, and appropriate breeding places.

d. Batrachoseps attenuatus. This is a specialized form with a slender cylindrical body and reduced appendages, and is capable of inhabiting worm-burrows and other small cavities in the ground. It spawns at, or near, the surface of the ground during the winter rainy period and the young hatch before the surface of the earth has become dried out by the heat of late spring. In the long dry summer period it is seldom found and is believed to take refuge then below the surface of the earth.

e. Ensatina eschscholtzii. This is a strictly terrestrial, lungless salamander which lives in damp situations at or near the surface of the ground. It breeds in late spring or during the summer months, seeking cavities under logs, or in burrows in the ground, where there is a constant humid local atmosphere. The female parent guards the

eggs and may keep them moistened with the contents of the bladder to prevent desiccation and keep down the growth of mold.

f. Aneides lugubris lugubris. This is a typical 'land' salamander, without either lungs or gills, which carries on its respiratory process in the throat and in the skin, particularly by means of large blood sinuses in the toes which are always in contact with the moist substratum of its habitat. It is strictly nocturnal. It is able to climb readily, and has been found abundantly in cavities in liveoaks. It spawns in moist chambers such as cavities on the ground beneath boxes in gardens, in spaces in hollow logs, and in rotted-out cavities in trees. The embryonic and larval stages are passed within the egg which is guarded against enemies and provided with moisture against desiccation by the female parent. Definite adaptations toward arboreal life are indicated in the prehensile tail and expanded digits. The maxillary and mandibular teeth are highly developed, possibly for service in protection against enemies. Use of fungus growing in oak trees as a source of food is indicated.

g. Scaphiopus hammondii. The spadefoot toad has the shortest larval period of any Salientian here discussed. The metamorphosed toad is provided with efficient digging 'spades' which are early put to use through instinctive action whereby the toad, in the presence of light (which in interior California means *heat*) digs into the ground and escapes desiccation. Spawning occurs in lowland areas with the advent of late spring rains whereby the eggs and larvae are provided with a high temperature resulting in rapid development. In elevated inland areas the spawning season comes in the summer months when thunder showers form pools in a time of high temperature.

h. Bufo boreas halophilus. The usual specializations exhibited by members of this genus elsewhere are observed in the California lowland form. These include small size of eggs, abundance of black pigment on eggs and larvae resulting in rapid development of both stages, and transformation at small size which permits of a short aquatic cycle. The egg complement is large to offset the various adverse conditions which beset the species, particularly in the earlier stages of its existence.

i. Hyla arenicolor. This species is restricted to the courses of boulder-strewn cañons in the mountains of the American southwest. Its present local distribution is discontinuous, though little or no local structural variation is observable, suggesting that the breaking up

of its range probably occurred in relatively recent geologic time. The entire life-cycle is spent along the stream. Spawning occurs late in the spring as with the other stream-inhabiting species discussed below, and for the same reason.

j. Hyla regilla. This is the most widely distributed and most adaptable of the species here studied. It inhabits a very wide geographic range and occurs under widely different conditions of temperature and humidity, yet is remarkably uniform in its structural features. Its coloration is highly modifiable and is usually found to match closely that of its immediate environment. Likewise in breeding activities the species shows greater variability than does any other form studied, a range of at least three months in spawning dates having been detected in one locality. Small size at transformation and small size of the adult are probably factors of importance in enabling the species to find suitable shelter in the many different habitats which it frequents.

k. Rana aurora draytonii. This, the largest of the native frogs, is highly aquatic and inhabits permanent pools of water. It spawns in the middle of the winter rainy period when the ponds are at their highest. These ponds seldom freeze, or, if they do, the ice does not last for more than a part of a day, so there is little or no danger to the species from low temperatures. The larval period is long, four or five months, a condition which is made possible by the permanency of the ponds inhabited. The egg complement is large.

l. Rana boylii boylii. [The remarks made here will probably be found to apply to *Rana boylii muscosa* of southern California, but no actual data on the life-history of that subspecies are available.] This frog inhabits only stream courses in the foothill districts of California. The adults are active for a considerable period before spawning, if indeed they have any inactive period at all during the winter months. Spawning is delayed until the peak load of water in the stream has passed, when the water is relatively free of sediment. Embryonic and larval development are compressed so as to be completed in the brief period between the advent of clear water and the time when the creeks become reduced to a series of small pools or else dry up completely. The adult is active by day as well as by night, probably because its haven of refuge, the creek, is available at all times and also because there is less danger of desiccation to an amphibian which at all times stays 'within one jump' of the water. The adult is of

small size which makes possible the use of small crevices and spaces under rocks for purpose of shelter. Small size of adults also means less growth to be accomplished between transformation from the larval stage and arrival at the breeding condition.

m. Rana catesbeiana. The Bullfrog native to eastern United States has been introduced in several localities in California where permanent pools are available and it seems to have taken hold and to be thriving here. So far as the imperfect data at hand show, its seasonal schedule here with regard to time of emergence from hibernation, time of spawning, and length of time required for larval development, conforms closely to its calendar in the eastern states and seems not, as yet, to have been modified by local conditions. Comparing this species with *Rana a. draytonii*, the native western 'bullfrog,' it would be expected that *catesbeiana* could here adopt a different schedule, and to its own advantage. But the fact that it evidently has not (so far as the few data at hand indicate) suggests that seasonal adjustment of stages in the life-cycles of amphibians are probably brought about by the action of natural selection through a long period of time. The general schedule is probably instinctive, the immediate schedule of any one year being dependent upon the particular conditions of temperature and moisture in that year.

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INDEX TO SCIENTIFIC NAMES

The pages upon which a particular species or subspecies is defined or treated in detail are printed in bold-face; synonyms are in italics.

Mere variations in the spelling of scientific names have not been listed separately in the index. Thus, Ambyostoma californiense and Ambystonia Californica, synonyms of Ambystoma californiense, are to be found under this name.

For purposes of a general index, consult the table of contents, and for the common (vernacular) names of species see the systematic list, pages 42–43.

EXPLANATION OF PLATES

NOTE.—The illustrations beyond are from negatives prepared by the author with these exceptions: Mr. C. L. Camp made that for fig. 22; Mr. Wright M. Pierce supplied the print for fig. 4; Mr. W. C. Matthews (under the author's direction) made the negatives for figures 19, 23, 25, 26, 28, 29, 36–39, 50, 52. Mr. Matthews also prepared all of the prints from which the half-tone blocks were made.

Where the figure legend is followed by a number the negative is in the photographic file of the Museum of Vertebrate Zoology; the remaining negatives are in the author's private collection except those for figures 1 and 18, which are in the file of the Zoological Laboratory, College of Agriculture.

PLATE 1

Fig. 1. Temporary pool in foothills, 2 miles west of Wallace, in San Joaquin County, photographed February 15, 1924. Spawning place of *Ambystoma californiense*.

Fig. 2. Portion of Costen Lake, 10 miles northwest of Ukiah, Mendocino County, photographed June 18, 1922. Spawning place of *Dicamptodon ensatus*. Used also by *Triturus torosus*.

Fig. 1

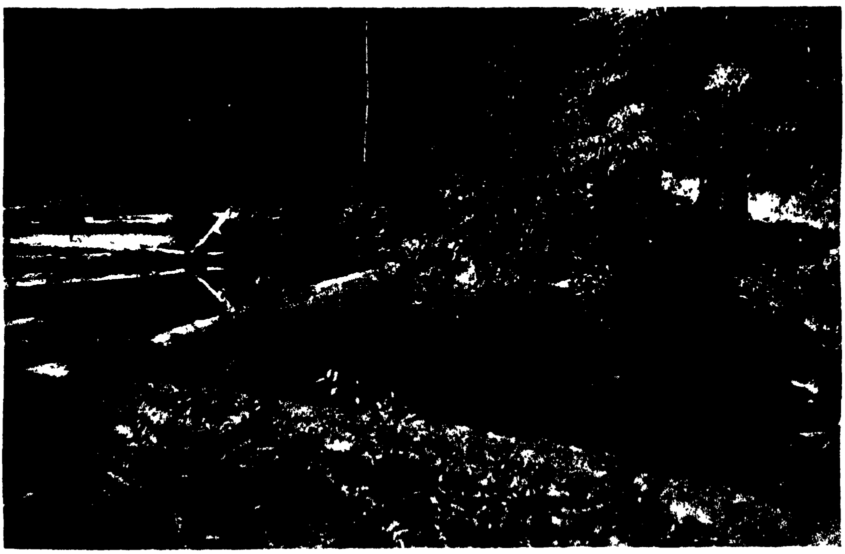


Fig. 2

PLATE 2

Fig. 3. Temporary surface pools in open country, 3 miles west of Santa Maria, Santa Barbara County, photographed April 10, 1923. Spawning place of *Scaphiopus hammondii*.

Fig. 4. San Gabriel Canon, Los Angeles County, photographed in August by Wright M. Pierce. Habitat of *Hyla arenicolor* and *Rana boylii muscosa;* probably also *Triturus torosus*.

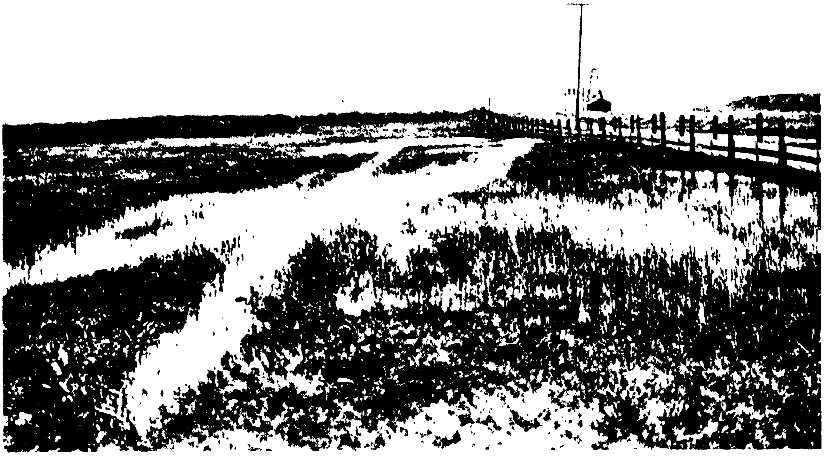


Fig. 3

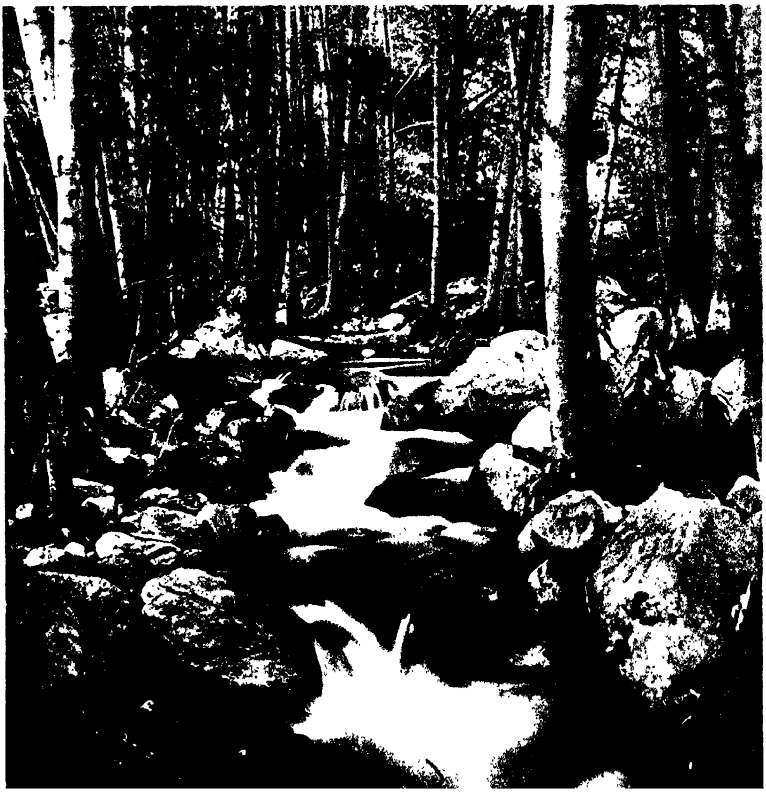


PLATE 3

Fig. 5. Thornhill pond, 3 miles southeast of Berkeley, Alameda County, photographed May 9, 1922. Spawning place of *Triturus torosus* along right hand margin, of *Hyla regilla* in far end, and of *Rana aurora draytonii* in left foreground.

Fig. 6. Papermill Creek near Tocaloma, Marin County, photographed May 5, 1923. Spawning place and permanent habitat of *Rana boylii boylii*; used also by *Triturus torosus*.

Fig. 5

Fig. 6

PLATE 4

Fig. 7. Permanent pool on Olema Creek marshes, ½ mile west of Point Reyes Station, Marin County, photographed May 6, 1923. Permanent habitat and spawning place of *Rana aurora draytonii*. Used also by *Dicamptodon ensatus*.

Fig. 8. Pool of New River, west of El Centro, Imperial County, photographed March 28, 1923. Habitat of *Rana pipiens*.

Fig. 7

Fig. 8

PLATE 5

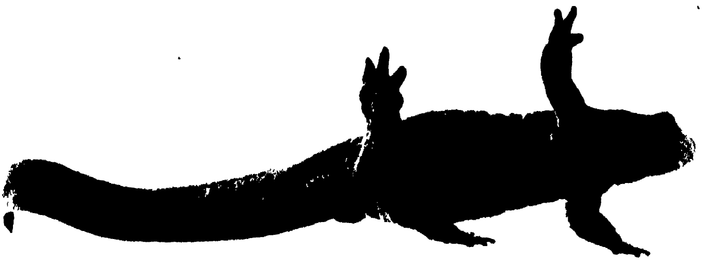
Triturus torosus, from vicinity of Berkeley, Alameda County.

Fig. 9. Terrestrial adult. Natural size.

Fig. 10. Aquatic adult male, in aquarium. About natural size.

Fig. 11. Egg masses as attached to twig in Thornhill pond, photographed January 6, 1922. About $^{13}/_{16}$ natural size. 3759.

9



10

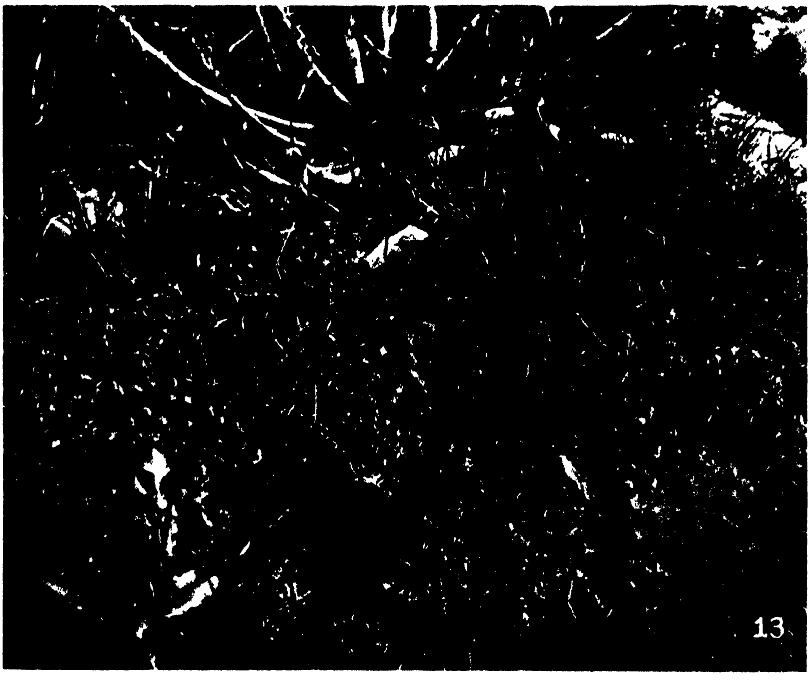
11

PLATE 6

Fig. 12. Larvae of *Triturus torosus*, *Hyla regilla*, and *Rana aurora draytonii*, all from Thornhill pond, 3 miles southeast of Berkeley, photographed February 14, 1921. Newt larvae with external gills, hylas with well-developed caudal fins, ranas just hatched. About 1⅝ times natural size. 3405.

Fig. 13. Egg masses of *Triturus torosus* exposed by receding water in Thornhill pond, February 14, 1914. 1180.

12



13

PLATE 7

Fig. 14. *Dicamptodon ensatus*, adult, from Santa Cruz County, photographed in 1913. Slightly less than ½ natural size. 2021.

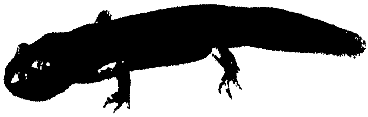
Fig. 15. *Ambystoma californiense*, larva, from Stockton, San Joaquin County, photographed April 26, 1922. About ½ natural size. 3770.

Fig. 16. *Ambystoma californiense*, newly transformed individual, from larva collected near Stockton; photographed May, 1923. Slightly under natural size.

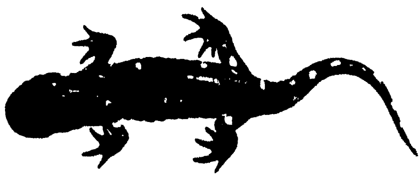
Fig. 17. *Ambystoma californiense*, adult, no. 7402, Mus. Vert. Zool., from Pacheco, Contra Costa County, photographed July 1, 1920. About ½ natural size. 3300.

14

15



16

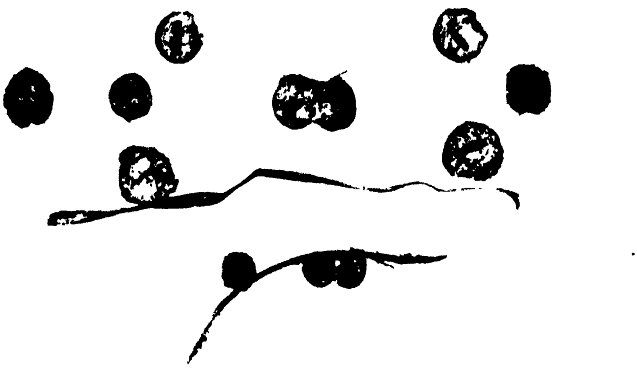


17

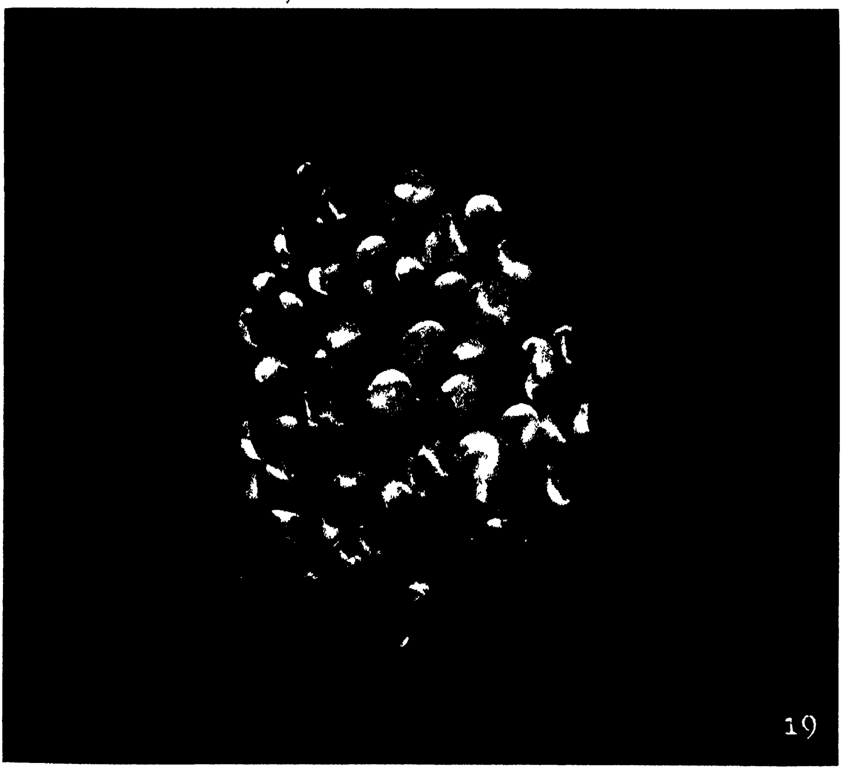
PLATE 8

Fig. 18. Eggs of *Ambystoma californiense*, from pool 2 miles west of Wallace, in San Joaquin County, collected February 15, 1924. About ¾ natural size.

Fig. 19. Egg mass of *Dicamptodon ensatus*, collected in Costen Lake, 10 miles northwest of Ukiah, Mendocino County, about February 20, 1924. Natural size.



18



19

PLATE 9

Plethodont salamanders.

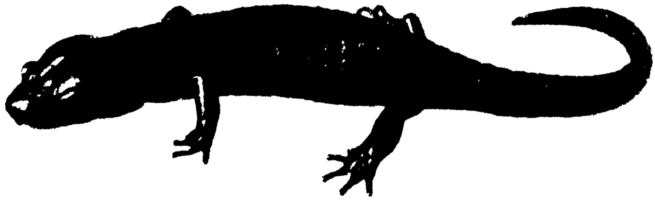
Fig. 20. *Aneides lugubris lugubris*, adult, from Berkeley, Alameda County, photographed May, 1923. Natural size.

Fig. 21. *Batrachoseps attenuatus*, adult, from Berkeley, Alameda County, photographed May, 1923. Natural size.

Fig. 22. *Ensatina eschscholtzii*, adult and eggs, from 6 miles west of Inverness, Marin County, collected and photographed June 4, 1913. About natural size. 1035.

Fig. 23. Eggs of *Ensatina eschscholtzii*, no. 9147, Mus. Vert. Zool., from Carlotta, Humboldt County, July 26, 1923. Natural size.

Fig. 24. *Batrachoseps attenuatus*, adult, in 'contracted' form, after being handled. Specimen from Berkeley, Alameda County, photographed February 21, 1921. Natural size. 3415.



20

21

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24

PLATE 10

Scaphiopus hammondii. All figures approximately natural size.

Fig. 25. Adult male. 3986.

Fig. 26. Adult female. 3985.

Fig. 27. Adult male in water to show webbing of feet. 3989.

Fig. 28. Adult male in act of croaking with vocal sac expanded; background and hand of operator painted out. 3987.

Fig. 29. Egg masses in advanced and early stages of development. 3984.

Fig. 30. Advanced stage of larva.

Material for figs. 25-29 from Santa Maria, Santa Barbara County, collected April 9 and 10, 1923; that for fig. 30 from Jenny Lind, Calaveras County, collected April 9, 1922.

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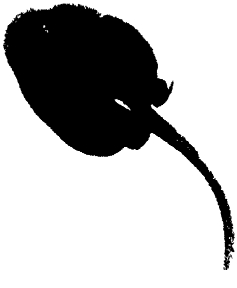

30

PLATE 11

Fig. 31*a*. *Bufo cognatus cognatus*, specimens from southeastern California. 2028.

Fig. 31*b*. *Bufo woodhousii*, nos. 1844 (left), 1843 (right), Mus. Vert. Zool.; specimens from Colorado River, at Potholes and 5 miles northeast of Yuma, Imperial County, collected April 27 and May 3, 1910; photographed April 20, 1913. About 3/4 natural size. 2028.

31a

31b

PLATE 12

Fig. 32. *Bufo alvarius*, adult, no. 8179, Mus. Vert. Zool., from Tolladay's Well, Maricopa County, Arizona, collected July 16, 1921. About 5/16 natural size. 3753.

Fig. 33. *Bufo boreas halophilus*, adult male from vicinity of Berkeley, Alameda County, collected and photographed April, 1913. About 7/16 natural size. 2027.

Fig. 34. *Rana boylii boylii*, male adult, from Salmon Creek, Mendocino County, photographed May 23, 1921. About 5/8 natural size. 3555.

Fig. 35. *Rana aurora draytonii*, no. 5612, Mus. Vert. Zool., from Berkeley, Alameda County, collected and photographed March 29, 1916. About 9/10 natural size. 2065.

Fig. 36. *Rana boylii muscosa*, male adult, from Eaton Cañon, near Altadena, Los Angeles County, photographed April 24, 1923. Slightly under natural size. 3992.


32


33


34


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36

PLATE 13

Hyla arenicolor. Natural size

Fig. 37. Adult female. 3995.

Fig. 38. Adult male. 3996.

Fig. 39. Eggs attached singly to sycamore leaf. 3994.

Material from Snow Creek, Riverside County, collected April 15, 1923.

37

38

39

PLATE 14

Fig. 40. *Hyla regilla*, adults, from Thornhill pond, 3 miles southeast of Berkeley, Alameda County, photographed February 9, 1921. ½ natural size. 3401.

Fig. 41. The same, ½ natural size. 3400.

Fig. 42. Eggs of *Hyla regilla*, from Thornhill pond, 3 miles southeast of Berkeley, February 9, 1921. ¾ natural size. 3399.

Fig. 43. Portion of egg complement of one female *Bufo boreas halophilus*, collected at Lafayette, Contra Costa County, May 22, 1921. About ⅜ natural size. 3559.

Fig. 44. Tadpoles, chiefly *Bufo boreas halophilus*, in shallow water of creek at Lafayette, Contra Costa County, May 14, 1921. 3560.

40

41

42

43

44

PLATE 15

Rana aurora draytonii

Figs. 45, 46. Adult female, no. 8577, Mus. Vert. Zool., from Dublin, Alameda County, collected May, 1922, photographed August 1, 1922. About 3/8 natural size. 3928, 3929.

Fig. 47. Complete egg mass, from Thornhill pond, 3 miles southeast of Berkeley, Alameda County, collected February 18, 1923. About 3/8 natural size. 3993.

Fig. 48. Three egg masses as grouped in Thornhill pond, photographed February 21, 1922.

45

46

47

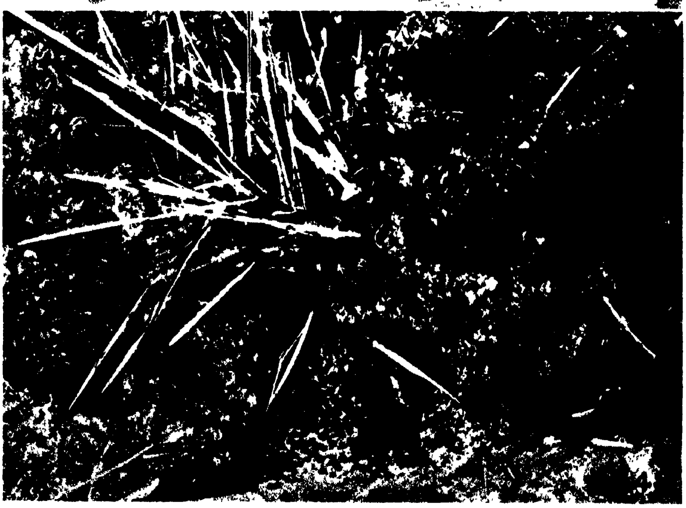

PLATE 16

Fig. 49. Larvae of *Hyla regilla* (upper left), *Rana boylii boylii* (upper right), and *Bufo boreas halophilus*, all approaching transformation; from creek at Lafayette, Contra Costa County, July 20, 1922. About 13/16 natural size. 3916.

Fig. 50. Egg mass (complete) of *Rana boylii boylii* from San Pablo Creek near Orinda, Contra Costa County, collected April 20, 1923. Natural size. 3990.

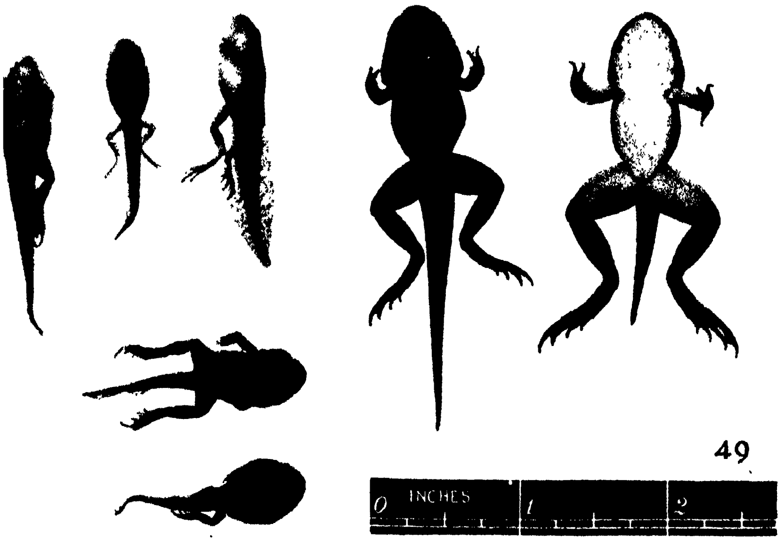

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PLATE 17

Fig. 51. *Rana boylii sierrae* and *Bufo canorus* (♀), from Porcupine Flat, Yosemite National Park, photographed June 27, 1915. $^{50}/_{100}$ natural size. 1690.

Fig. 52. Portion of fragmented egg mass of *Rana pipiens*, from 2 miles east of Dixieland, Imperial County, March 28, 1923, photographed after preservation. Natural size.

51

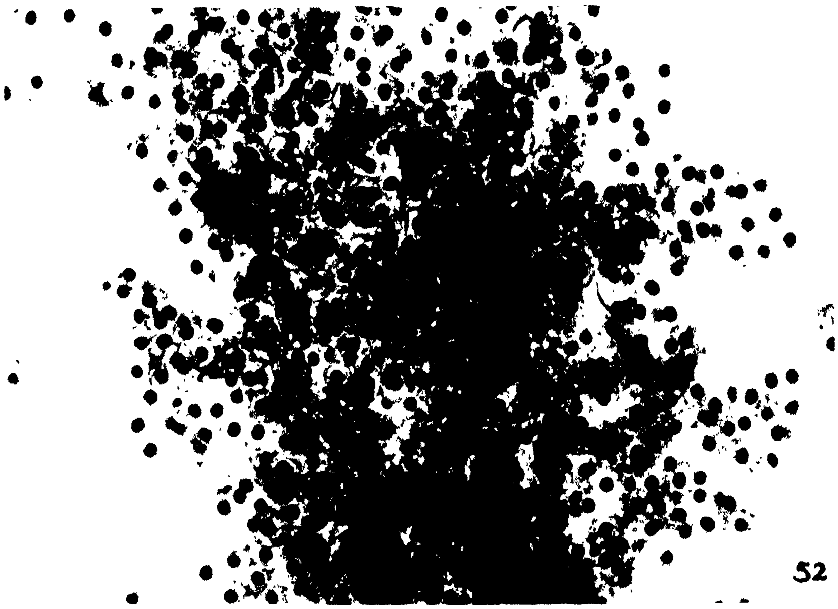

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PLATE 18

Rana catesbeiana

Fig. 53. Adult male, from near El Verano, Sonoma County, photographed July 12, 1922. About $\frac{7}{16}$ natural size. 3917.

Fig. 54. Second-year tadpole. About $\frac{3}{5}$ natural size.

Figs. 55–56. Adult female from near Riverside, Riverside County, photographed August 1, 1922. About $\frac{7}{16}$ natural size. 3923, 3924.

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Date of Issue	Date of Issue	Date of Issue

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